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## Vertebrate Fauna of North Carolina Coastal Islands

A Study in the Dynamics of Animal Distribution I. Ocracoke Island

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### Introduction

*Nature of problem.*—Zoogeographers usually recognize two chief types of islands, distinguishing between mainland islands and oceanic islands on the basis of their differing origins. A mainland island is a piece of higher land which has been cut off from the mainland through submergence of adjacent lowlands as a result either of subsidence of the land or elevation of the sea level. Its fauna is chiefly an inherited one coming directly from that which populated it while it was part of the parent land mass. An oceanic island, contrarily, is born of the sea bottom; it is barren on emergence, but subsequently acquires a flora and a fauna through waifs and drifts arriving over, on, or through the water, often from considerable distances and from a variety of sources. The fauna of a mainland island is usually balanced and homogeneous, although impoverished in comparison with its mainland; that of an oceanic island is heterogeneous, because of its diverse origins, and the various systematic groups are disproportionately represented.

Along much of the Atlantic coast of North America south of Cape Cod, along the low countries bordering the North and Baltic seas, and in a few other parts of the world, there occur narrow islands, lying parallel to the main coast and separated from it by salt marshes and tidal creeks or by wide, shallow bodies of water; these are the so-called "barrier-beaches," "outer

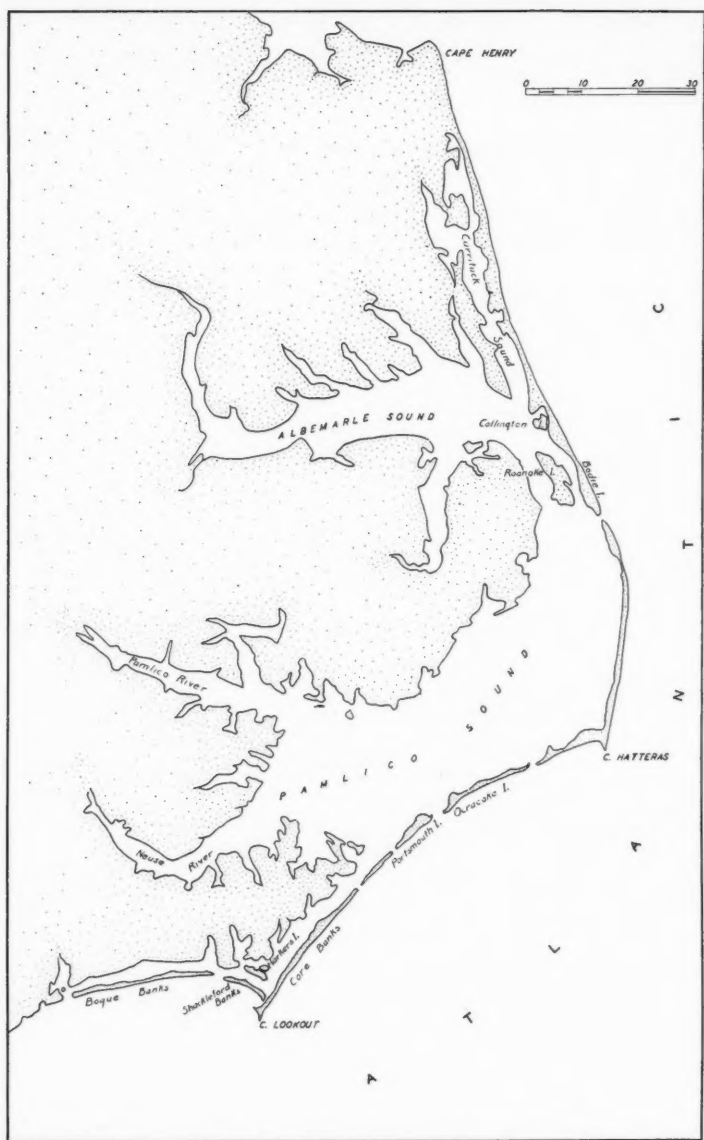


Fig. 1. Map of portion of the Atlantic coastal region of North America, from Chesapeake Bay to a point about 100 miles above Cape Fear, and including all of the North Carolina "outer banks."



beaches," "sandy reefs," or, more properly, *offshore bars*. They resemble true oceanic islands in their origin from the sea bottom (Johnson, 1919); they differ from the usual oceanic island in that they are formed close to a mainland, in a long series parallel to its coast and, therefore, present to this near, neighboring mainland a lengthy and almost continuous shoreline. It is evident from the resulting topographical relation to the mainland that in its initial stages of development the offshore bar is at once more accessible to an invading population than is the usual type of oceanic island, but hardly accessible from any source other than the immediately adjacent mainland. In this same way (easily accessible, but from a restricted source) it resembles a mainland island; but it differs from the latter in that its eventual fauna, like that of an oceanic island, is altogether an acquired one, which has to reach the bar subsequent to the emergence of the bar from the sea bottom. In the later, mature stages, however, where the bars have been forced back against the mainland, they become even more directly accessible to the mainland fauna.

We have here, then, a particular and peculiar zoogeographic situation, which seems to offer distinct possibilities for the clarification of dynamic principles of geographic distribution. With this in mind, I have undertaken to make an analytical study of a typical series of such offshore bars, namely those which fringe the North Carolina coast from Cape Henry to Cape Lookout, forming the outer rim of Currituck, Albemarle and Pamlico Sounds, and known locally as the "outer banks." The study was limited from the beginning to tetrapod vertebrates, exclusive of the shore- and aquatic birds and exclusive of all birds not present during the breeding (summer) season. The aims were first to discover which species have become established on the various islands, and later to study the differentiation, if any, of the individual populations.

The present paper describes the vertebrate fauna of the most centrally located bar in this series of islands. I hope to discuss the fauna and particular conditions of other islands in later papers, as the work progresses.

*Age of the islands.*—Nothing more definite can be said at present regarding the age of these bars than that they almost certainly are post-Pleistocene in origin. It is probable that they are not more than 20,000—nor less than 5,000—years old.

*Geography and topography of Ocracoke Island.*<sup>1</sup>—Ocracoke lies off the

<sup>1</sup> In all, thirty-six days were spent on the island in the summers of 1940 and 1941 and two days in the spring of 1942. In 1940, two days were spent at the village of Ocracoke (June 9, July 6): then for twenty days, from June 16 to July 5, I occupied "Dick's Camp" at the Knoll, approximately in the center of the island, from which I was able to cover thoroughly the whole area from the Plains to the far side of the Great Swash; we returned to this camp for fourteen days in 1941 (June 7-June 21). (For localities see Fig. 2a and 2 b). I am grateful for the cheerful companionship as well as the assistance of Dr. Richard A. Edwards and Helen Stoddard Edwards who were with me at Dick's Camp both summers. Mr. Richard O'Neal and Mr. Wahab Howard, both of Ocracoke, were extremely hospitable, aiding us in ways too numerous to mention. Mr. O'Neal, retired coast guards man, also gave us much information as to former conditions on the island. Laurie Stewart Radford and Albert E. Radford of the Herbarium of the University of North Carolina kindly identified plant specimens for me.

OCRACOE ISLAND  
NORTH CAROLINA



Fig. 2a. Topographic map of Ocracoke Island, approximate scale 1:160,000. Adapted from U. S. Coast and Geodetic Survey, Topographic Survey no. T3662, 1916.

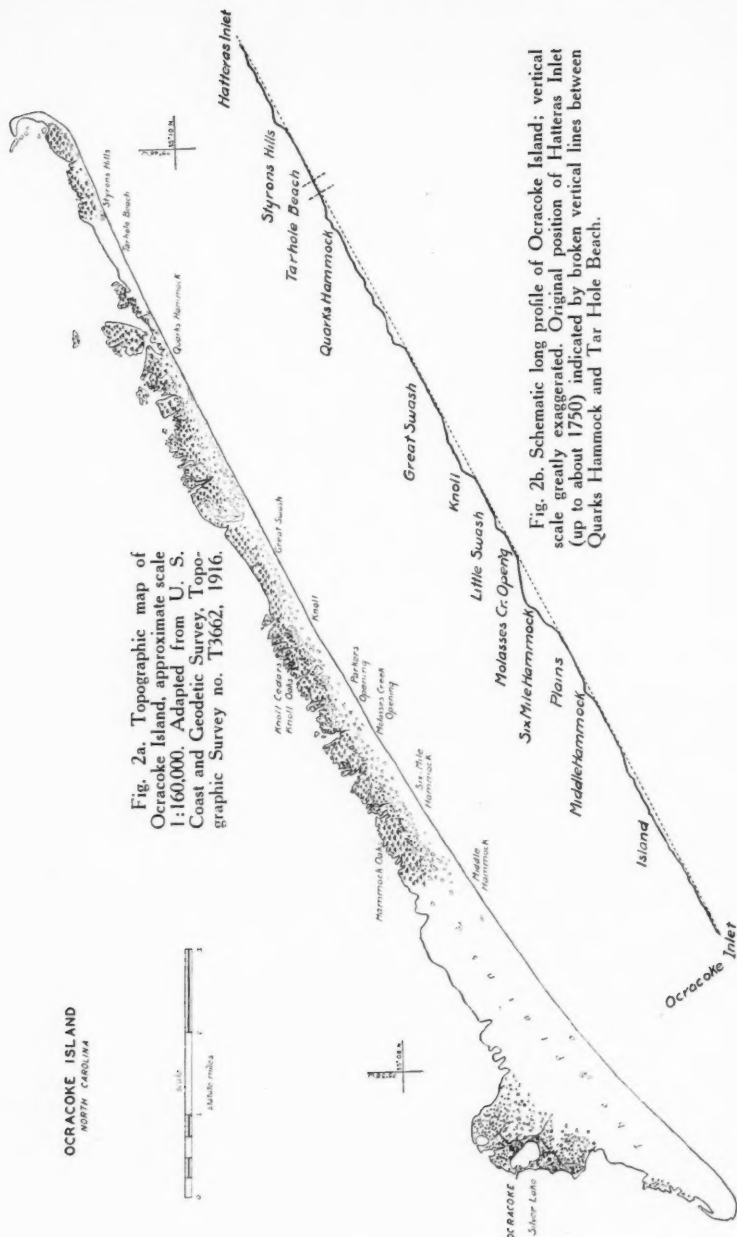


Fig. 2b. Schematic long profile of Ocracoke Island; vertical scale greatly exaggerated. Original position of Hatteras Inlet (up to about 1750) indicated by broken vertical lines between Quarks Hammock and Tar Hole Beach.

coast of North Carolina nearly opposite the mouth of the Pamlico River and approximately 30 miles from the nearest point on the mainland (Fig. 1). One of the chain of islands forming the "barrier beach" which rims the Carolina coast, it is separated from the adjacent Hatteras Island, to the northeast, by Hatteras Inlet, and from Portsmouth Island, to the southwest, by Ocracoke Inlet; through these two inlets the tide pours back and forth between Pamlico Sound and the Atlantic Ocean. The long axis of this narrow bar extends southwesterly from neighboring Cape Hatteras, roughly parallel to the mainland coast, approximately to longitude  $76^{\circ}$  west, latitude  $35^{\circ}$  north.

Through the greater part of its length of 17 miles, Ocracoke is only about  $\frac{1}{2}$  mile wide (Fig. 2a); near the southwest end it is at one point nearly two miles in width, but for a considerable distance, toward Hatteras Inlet, barely 200 yards separate the sound from the sea (Fig. 9). Much of the island is less than one foot above sea level; little of it rises more than three feet above the sea. The dunes scarcely exceed 20 feet in elevation—most of them are much lower; they occur as scattered, isolated hills of sand, or as small clusters of hills, not forming a continuous barrier to the encroachment of the sea.

The southwesterly fourth of the island is made up of a continuous sandy flat, known locally as the Plains, and a blunt projection into Pamlico Sound, enclosing a small lagoon (Silver Lake), which is slightly higher than the barely emerged flat of the Plains. Here are clustered the homes, stores, churches, coast guard station, and lighthouse that together make up the only community on the island. The Plains are completely barren—a sandy waste—frequently flooded by winter storm tides or by northerly gales blowing the water out of Pamlico Sound. The Plains thus isolate the community from the remainder of the bar—the community is indeed spoken of by all the natives as "the Island." Northeastly from the Plains, Ocracoke has the typical profile of an offshore bar: back of the barren outer beach is an irregular line of dunes, behind which a relatively broad marsh extends to the shore of the sound. This marsh is cut up by numerous tidal creeks, a few of which reach between the dunes almost to the outer beach. Since the water level in Pamlico Sound is influenced more by wind than by tide, the amount of water in these creeks is dependent on wind direction—some of them are extremely low, exposing mud banks for days on end during the prevailing southwesterly winds of summer, but a shift of the wind to the north fills them up overnight. The water level on the marsh is subject to the same influence.

The entire bar may be visualized as a low, barely emerged shoal, from which the dunes arise as a series of hammocks (Fig. 2b). The flat, low intervals between the hammocks average considerably less than two feet above mean water level; from a short distance out on the sound or sea these flats or "openings" disappear from view, the bar then taking on the appearance of a series of small islands. Two of the openings—the Plains and the Tar Hole Beach—are indeed commonly flooded by the highest tides.

*Recent physiographic history.*—Within relatively recent times Ocracoke was physiographically very different. The lower, southwest end appears to have been a small, isolated island separated, as now, from Portsmouth by Ocracoke Inlet, but separated also from the middle section of the present island by an inlet over what is now the Plains. To the northeast of this middle section, "Hatteras Inlet" flowed across the bar just beyond Quarks Hammock, across the lower end of the present Tar Hole Beach. The extreme northeast section of the island, three to five miles in length, was a part of Hatteras Island, continuous with the bar which includes Cape Hatteras.

The existence of a "Hatteras Inlet" in early post-Columbian times is indisputable, on the testimony of numerous early mariners' charts. However, Price in 1795, describing Ocracoke Inlet and its approaches, says that

Cape Hatteras and the land from it toward Occacock [Ocracoke] to the distance of about thirteen miles, are covered with large evergreen trees, such as live-oak, pine and cedar. Here are three large and remarkable sand hills, called Stowe's Hills [Styrons Hills]. The coast afterward is a bald beach, interspersed with a few low sand hills; about eleven miles farther is a group of trees, called the Six-Mile Hammock, from its distance from Occacock—from thence the coast is quite barren and sandy....

Surely a guide for mariners "adorned with a map taken by actual survey" (Price, 1795), describing the coast from Cape Hatteras to Ocracoke Inlet, could not have failed to mention an opening in the bar between these points, if such existed.

Welch (1885) has gathered the only available evidence as to the probable time of closing of the old Hatteras Inlet, which he puts at about 1750. He cites first a "Chart of the Coast of America from Cape Hatteras to Cape Roman from the actual Surveys of Daniel Dunbabin, Esq.," first published in 1764, later "bound in with others in *The American Pilot*, published at Boston by William Norman, Book and Chart Seller..." which shows no inlet between Cape Hatteras and Ocracoke. Contemporary charts which did show such an inlet Welch justifiably concludes to have been copies of the chart of Wimble (1738) or "some other older chart." His remaining evidence was received, second-hand, from two natives, one in his 75th year at the time (1885), the other in his 72nd year, both born and raised in the vicinity of the present inlet. The story of the one, corroborated by that of the other, was that he had heard his grandfather, who died in 1825, age 86, say that there had been an inlet about six miles from the present inlet; that an English ship ran aground on the bar of this inlet and was lost; that the wreck sanded up and the beach made down to it, finally closing up the inlet.

On the testimony of Welch's correspondent, a licensed pilot for Ocracoke Inlet who lived in Hatteras, the present Hatteras Inlet was cut out by a violent storm on Sept. 7, 1846.

The evidence is, then, that the northeastern three to five miles of the present Ocracoke Island, from the lower end of the Tar Hole Beach to Hatteras Inlet, was the southwestern end of Hatteras Island up to about 1750, that it became cut off from Hatteras Island in 1846, having been a connecting

link between Hatteras and Ocracoke in the intervening century, and that it has been joined to the rest of Ocracoke Island for about two hundred years.

The history of the Plains surrounding the village of Ocracoke is obscure. Price (1795) says that

Occacock was heretofore, and still retains the name of, an island. It is now a peninsula; a heap of sand having filled up the space which divided it from the bank.

It is clear that Price is speaking of the region of the community, and that the "heap of sand" is the Plains; but it may be questioned whether his statement that Ocracoke "was heretofore. . . an island" was based on knowledge or on inference from topography.

These physiographic changes have obvious significance zoogeographically, in that they indicate possibility of transfer of fauna from one island in the chain to the next through what might be called a "flanking invasion," or "lateral migration" along the bars, over land bridges rather than across water barriers. But in this particular instance, as will appear especially in the discussion of the mammalian fauna (p. 296), the merger of Hatteras and Ocracoke Islands and the subsequent transfer to the latter of part of the former has had little if any influence on the faunas of the Ocracoke fauna.

*Vegetation.*<sup>2</sup>—The more obvious aspects of the plant cover, which determine in large part the distribution of the vertebrates present and in some measure the presence or absence of certain forms, are those characterized by the general terms "woods," "thickets," "marsh," "meadow," and the very distinctive cover (sea oats) of the dunes, for which no general term is available.

The outer beach, like the Plains and the Tar Hole Beach, is barren—a flat waste of sand and broken shell. Thirty to fifty yards back from the high-water line are the outermost dunes, insecurely stabilized by the root stalks of the sea oats, *Uniola paniculata*. This tall, lovely grass, the stems rising from 3 to 5 feet each out of a clump of long thin leaves, is one of the most characteristic vegetational types of the island (Fig. 3). More widely spaced

<sup>2</sup> The vegetation of Ocracoke has been described by Kearney (1900) and classified as follows:

I. Sand-strand vegetation.

1. Treeless (open).

a) Beach formation: *Croton-Physalis* association.

b) Dune formation: *Uniola-Yucca* association.

2. Evergreen trees and shrubs.

a) Tree formation: *Quercus virginiana* association.

b) Thicket formation: *Ilex vomitoria* association.

II. Salt-marsh vegetation.

1. Creek-marsh (closed) formation.

a) *Spartina stricta* association.

b) *Juncus roemerianus* association.

2. Dune-marsh formation: *Lippia-Monniera* association.

3. Tidal flat (open) formation: *Sesuvium-Tissa* association.

III. Pastures and ruderal plants.

IV. Cultivated plants."



Fig. 3. Upper: Scrub wax myrtle (*Myrica*) and sea oats (*Uniola*) on side of dune at the Knoll, July 4, 1940. Lower: Wax myrtle and sea oats, insecurely holding the northwest side of a dune; roots of the wax myrtle exposed by blow-out. The Knoll, July 4, 1940.

on the outer dunes, it forms a dense cover on the tops and leeward slopes of those less exposed. Associated with this grass is a small cactus, *Opuntia pes-corvi*, often painfully common, and, except on the outermost dunes, usually a few small individuals of the Spanish dagger, *Yucca gloriosa* (Fig. 4).

Between and behind the outer dunes is a very scanty beach vegetation, scattered individuals of just a few species, including the seaside evening primrose, *Oenothera humifusa*, and the prostrate seaside spurge, *Euphorbia polygonifolia*.

Back of the dunes, the sea oats give way to dense thickets, 1 to 10 feet high. The taller portions of the thickets are composed solely of a deciduous holly, the yaupon, *Ilex vomitoria*. Associated with the yaupon-holly and often forming pure-stand thickets, are the pungently fragrant wax myrtle or bayberry, *Myrica cerifera*, and the very thorny southern prickly ash or toothache tree, *Xanthoxylum Clava-Herculis*. These thickets tend to form a continuous margin between dunes and marsh on the drier, sandier ground where the inner border of the marsh is being covered and the soil level raised as a result of deposition of sand blown over from the dune area by the southwesterly winds prevailing in spring and summer. But many isolated thickets, a few feet to several yards across, are scattered over the inner part of the dune area, among the sea oats (Fig. 4, upper), in some protected places climbing up the back slope of the dune to the very top. The thickets have a very distinctive shape, sloping gradually upward along a southwest-northeast axis. This characteristic "wind form" has been reinterpreted by Wells and Shunk (1938) as a "spray form," the result of killing action of salt spray during the growing period.

Small tree-covered areas are scattered between the dense marginal thickets and the marsh, or in higher places within the thickets. These woods are made up of almost pure stands of live oak, *Quercus virginiana*, with an occasional red cedar, *Juniperus virginiana* (Fig. 5, lower). There was formerly a pure stand of very large red cedars, covering several acres, just east of the Knoll, called the Knoll Cedars; very few of these now survive, but many of the dead trunks are still standing and a few of these support such luxuriant vines of poison ivy, *Rhus radicans*, as to give the appearance of live trees with a dense crown (Fig. 5, upper). On swampy ground between thickets and marsh is an occasional red bay, *Persea*; these form a definite woodland only for a short distance between the Plains and the Hammock. In addition to these red bays and the Knoll Cedars, there are only three small woods between the Plains and the Great Swash: the Hammock Oaks, a group of fine old trees covering perhaps an acre, and two smaller stands of live oaks, one between the Hammock and the Plains, and one just west of the Knoll, called the Knoll Oaks; there are no trees anywhere between the Great Swash and Hatteras Inlet. The "Island," site of the community surrounded by the barren Plains, is also wooded, with the live oak predominant. Thickets and beach vegetation fringe this isolated area (Fig. 6).

Back of the thickets and scattered woods, the salt marsh extends to the shore of Pamlico Sound (Fig. 7, lower). The greater part of the marsh from



Fig. 4. Upper: Dune thickets (wax myrtle, *Xanthoxylum*, and yaupon-holly) scattered among the sea oats back of the dunes; note characteristic slope (cf. text). The large cactus is not native. Parkers Place, between Parkers Creek and Parkers Opening, July 4, 1940. Lower: Spanish dagger (*Yucca gloriosa*) on back and top of dune. The Knoll, July 4, 1940.





Fig. 5. Upper: The Knoll Cedars, a dead *Juniperus* forest, growing up to marsh elder (*Iva frutescens*); some wax myrtle and yaupon-holly. July 5, 1940. Lower: *Quercus virginiana*, the Hammock Oaks. Large vines of poison ivy climbing the two oaks at the right. July 1, 1940.



Fig. 6. Upper: Yaupon-holly, red cedar, and skeletons of live oak; characteristic wind-form, sloping upward on southwest-northeast axis. North shore of Silver Lake, March 19, 1942. Lower: Yaupon-holly and wax myrtle thickets; beach vegetation in foreground. Shore of Pamlico Sound at Spring Point, about 1 mile south of Silver Lake, June 9, 1940.

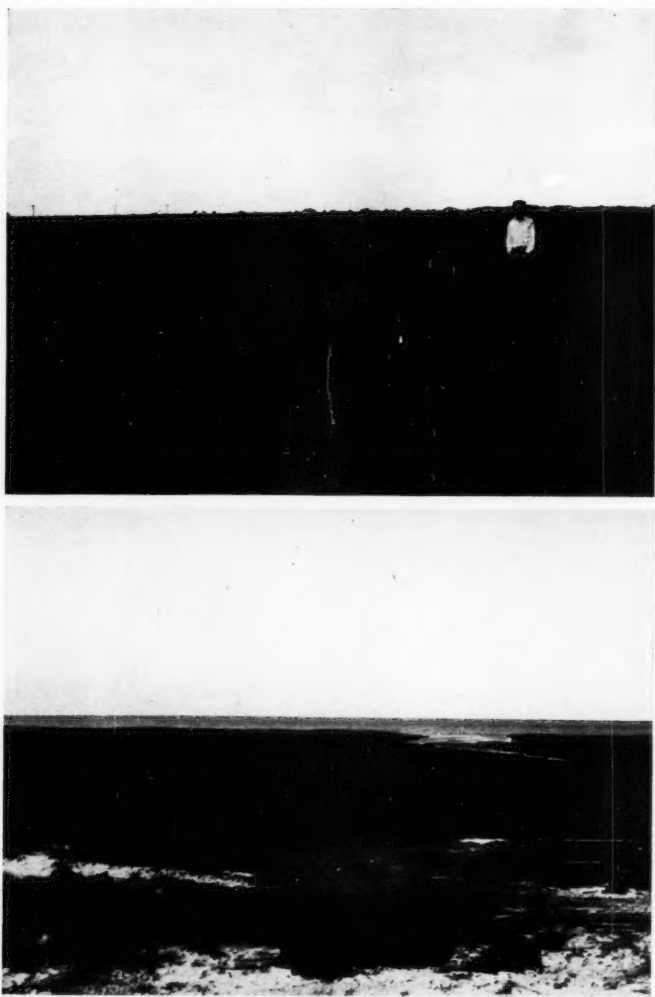


Fig. 7. Upper: Spike rush (*Juncus*) and marsh elder (*Iva frutescens*) on north side of Parkers Opening; dunes on horizon between Parkers Opening and Molasses Creek Opening. July 4, 1940. Lower: Marsh, back of Dick's Camp at the Knoll; foreground: edge of dune area, low thickets of wax myrtle and *Xanthoxylum*; middle: inner edge of marsh, dotted with marsh elder; background: spike rush (*Juncus*) marsh, mouth of Try-yard Creek, and Pamlico Sound. June 30, 1940.



Fig. 8. Thickets (yaupon-holly) invading marsh, to the left; edge of the Knoll Cedars at the right; center: marsh elder and spike rush, July 5, 1940.

the Plains to the Great Swash is composed of a dense stand of nearly waist-high, stiff, reed-like and needle-sharp spike rush, *Juncus roemerianus*. Patches of the salt-marsh grass, *Spartina glabra*, occur scattered through the spike rush in wetter places and form a fairly definite outer margin to the marsh, bordering the Sound and the larger creeks near their mouths. Here also are frequent patches of glasswort or samphire, *Salicornia* sp., and the seashore salt grass, *Distichlis spicata*. The marsh is everywhere intersected by the numerous tidal creeks and pitted with shallow, muck-bottomed pools.

All along its inner edge, the marsh is invaded by thickets, usually of the yaupon-holly *Ilex vomitoria* (Fig. 8). The shrubby marsh elder, *Iva frutescens*, also frequently dots the higher areas within the spike rush marsh, sometimes forming a close cover almost to the exclusion of the *Juncus*.

Certain meadow-like areas, covered with a dense, mostly less than knee-high growth of grasses and similar vegetational forms, remain to be mentioned. At intervals along the length of the bar, these interrupt the sequence of types of plant cover outlined above and, extending from the dune area across the width of the island to the sound, replace the thickets, woodland, and spike rush marsh (Fig. 7, upper). Colloquially they are called "openings" or "swashes"; with some doubt I refer them to the "tidal flats" of Kearney (1900).<sup>3</sup> There are three major areas of this type: Molasses Creek Opening, Parkers Opening or Little Swash, and the Great Swash. The first two extend each about a mile along the long axis of the island; the Great Swash is about two miles long. The latter is especially interesting, since I am assured by older natives that 40 to 50 years ago it was a sandy flat, as barren as the Plains, absolutely devoid of vegetation. Along the shore of the Sound is an almost pure growth of the seaside salt grass, *Distichlis spicata*, interrupted here and there by extensive patches of the glasswort, *Salicornia*. These extend some distance toward the center of the bar; the soil is moist, and under a northerly wind is covered with water to a depth of 2 to 3 inches. With a rise in soil level of just a few inches, the aspect of the vegetation changes sharply, and the rest of the swash is densely covered by a variety of grasses, sedges, etc. among which are a species of *Scirpus* (= *americanus*?) growing in tough clumps; the cord grass, *Spartina patens*; foxtail grass, *Setaria lutescens*; the spike "rush," *Eleocharis rostellata*; a species of the sedge, *Dichromena*; the fog-fruit, *Lippia nodiflora*; the water pimpernel, *Samolus floribundus*; the buttonweed, *Diodia virginiana* and others. None of the thicket forms are represented; the only shrub is an occasional marsh elder, *Iva frutescens*. Molasses Creek Opening and Parkers Opening are similar, except that toward

<sup>3</sup> That these "swashes" are not recognizably referred to by Kearney seems to indicate that in his short visit (only 5 days) his investigations may have been confined to the neighborhood of the community and that he did not do any extensive collecting beyond the Plains. In this connection, it is also noteworthy that in his discussion of the "tree formation" he says of *Juniperus virginianus* only that it is "occasionally" found with the live oaks, although at this time (1900) the Knoll Cedars, a large grove of *Juniperus* in a pure stand, some seven miles from the village, must have been one of the most impressive pieces of woodland on the island. There was also a growth of cedars between Styrons Hills and Hatteras Inlet at that time.

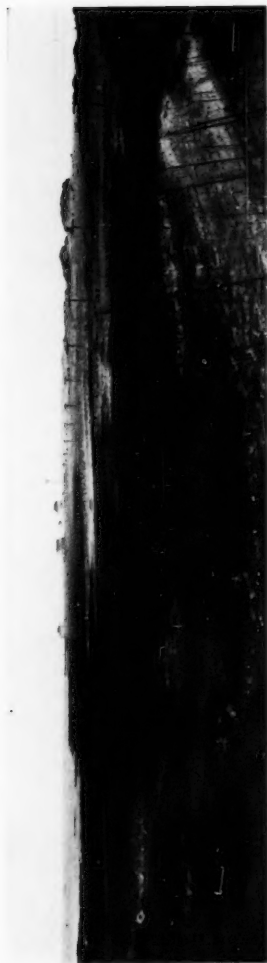


Fig. 9. Northeast end of Ocracoke Island, from Styrons Hills, looking toward Hatteras Inlet; entire width of island is shown. Note characteristic form of an offshore bar: (from right to left) outer beach, dunes sloping back, passing over into marsh which extends to shore of sound. Blow-over of sand from dune area onto marsh clearly shown in center. Dune thickets and marginal marsh thickets absent from this area now, but formerly extensively developed at this place. Hatteras Inlet Coast Guard Station in background. March 18, 1942.



Fig. 10. Styrons Hills rising out of the Tar Hole Beach; ocean to the right, sound at extreme left. Storm tides frequently flood this flat. Formerly, up to about 1750, not a part of Ocracoke, but the lower end of Hatteras Island. (Cf. text, pages 278, 279). March 19, 1942.

the Sound there are typical *Juncus* salt marshes, *Juncus* being almost totally absent from the Great Swash. Toward the dunes the vegetation becomes sparse, and with an elevation between two and three feet above the sea passes over into a beach vegetation, mingled with sea oats (*Uniola*).

To summarize, the vegetational cover of Ocracoke Island offers the following general picture (Fig. 9) in sequence from ocean to sound: a scanty beach vegetation first appears between and behind the outermost dunes, the wide and flat upper beach bordering the ocean shore being completely barren; a sparse covering of sea oats on the outer dunes gives way on the inner dunes then to a dense cover of sea oats with some yucca and cactus; sea oats also cover the sandy area back of the dunes, but small thickets are scattered over it also; a continuous line of thickets is developed along the inner edge of the sandy area, where this gives way to salt marsh, occasionally forming a thicket-woodland; straggling thickets extend out into the marsh from these marginal thickets, but the marsh is covered chiefly with spike rushes, and is bisected by numerous creeks and pitted with pools; this sequence is sometimes interrupted by barren sandy flats extending from outer beach to sound (Fig. 10) or by meadow-like openings extending from the dune area to the sound.

*Climate.*—The exposed position of Ocracoke Island has a marked influence on its climate. The waters of the ocean and Pamlico Sound combine to effect lesser diurnal and seasonal temperature changes on the island than on the adjacent mainland, and a greater amount of precipitation. Data are not available for Ocracoke itself, but from the station at Hatteras, immediately across narrow Hatteras Inlet from Ocracoke Island, we have continuous records since 1874 (U. S. Weather Bureau, 1933). The accompanying climograph (Fig. 11) indicates the climate at Hatteras station with respect to monthly average temperature and precipitation. The relatively mild temperatures are emphasized by the seasonal averages—winter, 47° F.; spring 59°; summer 77°; and fall, 65°. The highest temperature ever recorded here was 93°, the lowest 8° above zero. On the average, 90° is reached but once per year, 32° or lower on only 16 days each year. The difference between the annual average maximum temperature and annual average minimum (12° F.) is indicative of the relatively small daily swing between extreme temperatures.

The rainfall is almost evenly distributed throughout the year, but is slightly heavier in the summer months.<sup>4</sup>

Very characteristic are the strong winds that sweep almost constantly over the island. At Hatteras station the average wind velocity is 13.4 miles per hour over the entire year, ranging from an average of 11.2 m. p. h. in August to 15.0 m. p. h. in March. Winds in excess of 49 m. p. h. have been recorded for every month except May (high of 44 m. p. h.). The prevailing winds

<sup>4</sup> The precipitation data from Hatteras seem to indicate an approximately 70-year cycle in amount of rainfall. Averages for the first six decades following the establishment of the station are as follows: 1875-1884, 74.5 inches annually; 1885-1894, 58.6 in.; 1895-1904, 50.9 in.; 1905-1914, 43.8 in.; 1915-1924, 47.4 in.; 1925-1934, 52.7 in.; (and 1935-1938, 54.1 in.).

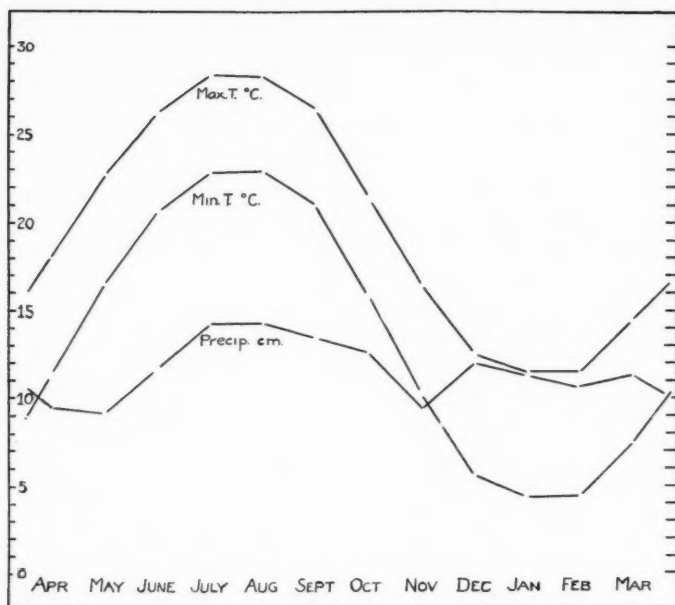


Fig. 11. Temperature-precipitation chart for Hatteras, N. C. Data from U. S. Weather Bureau, 1933. Average daily maximum and minimum temperatures by month and total monthly precipitation.

are from the northeast in the fall, from the north in winter and from the southwest during spring and summer.

The exposure of the island, and its relation to principal storm paths, make it subject periodically to violent storms. These storms may be accompanied by heavy rainfall (a high 72-hour record of 9.76 inches, June 25-June 28, 1919); but their great destructive power is due to the high winds (up to 80 m. p. h., as on August 17, 1899) and tidal floods. Ocracoke Island, especially, is subject to being overrun by the sea, because of its low elevation and its generally low relief. During the hurricane of September, 1933, the entire village of Ocracoke was under from 1 to 4 feet of water. During such storms only the dunes project above the surface of the sea and all natural land habitats, except these, are covered by salt water. When the storm abates, the impounded flood-waters of the Sound rush back out to the sea, scouring over the island, uprooting brush and trees and undercutting the dunes. Storms such as these occur about once every decade.

*Instability of topography and vegetation.*—There is generally prevalent an idea that the present tendency to erosion of "barrier beaches," such as Ocracoke,



is due primarily if not exclusively to the activities of man, including grazing of his cattle (see, for example, Oosting and Billings, 1942); but there is abundant evidence that instability is a prime characteristic of an off-shore bar, that those very forces which brought the bar into being tear at its seaward face, forcing it gradually back against the mainland (cf. Johnson, 1919). Added to this slow erosion of the seaward beach is the destructive action of periodical hurricanes and their accompanying floods. Thus in 1931, when Mr. Richard O'Neal built in the shelter of the dunes at the Knoll the small cabin now generally called Dick's Camp, the marginal thickets were so tall and dense that the Camp could not be seen from the marsh behind it. At the time of our first visit in 1940 there was no sign here of thickets (Fig. 7, lower), and the house could be seen clearly not only from the marsh but even from far out on the Sound. Meanwhile there had been no cutting, but there had occurred two unusually violent storms, in the autumns of 1933 and 1937.

Obviously the Knoll Cedars were not doomed by cutting; the stout skeletons of this dead forest (Fig. 5, upper; Fig. 8) bear testimony to a more natural death. Fifty years ago a similar dead *Juniperus* woodland stood just north of the Great Swash—the locality is still known as the "Scraggly Cedars"—but these skeletons have since disappeared entirely, thus forecasting the not distant day when the stranger will wonder why a treeless piece of dune and marsh should be called the "Knoll Cedars." Beyond Styrons Hills, to Hatteras Inlet, there was likewise formerly a thick growth of yaupon-holly, live oak and red cedar, of which now not a stub or stump remains (Fig. 10). At the Middle Hammock, lying isolated in the Plains, there was also a thicket woodland which has now completely disappeared, leaving only a few small dunes with their cover of sea-oats, surrounded by an absolutely barren sandy waste.

It cannot be doubted, however, that human activity has contributed to and hastened the progress of this natural process of change. In a fenced area of several acres near the Knoll, protected from the ponies and the cattle, the thickets are notably denser than elsewhere, and here one frequently sees sapling red cedars, which are otherwise extremely uncommon on the island.

In one locality only, the Great Swash, has a change occurred in the opposite direction, toward construction rather than destruction. Up to about 1900, the Great Swash, as the name implies, was a barren flat, exactly like the Plains and the Tar Hole Beach; like them it was a true "opening," without dunes on its seaward side. What happened then as a cause of change is now irretrievably lost, but through some accident of shipwreck or meteorological vagary some dunes were built up along the outer beach and these were followed soon by the appearance of marsh grasses and sea oats; the whole then was relatively quickly built up, and the Great Swash today, as described above, is a long meadow-like area covered with a thick, lush growth. This is the more notable because of the recent conspicuous failure of man to bring about a similar result on the Plains and the Tar Hole Beach in a Federally sponsored beach erosion control project (1936-1939).

Since the name "swash" implies a shoal, periodically emergent, but over which the water sometimes "swashes," and since place names, once given, are retained long after they have ceased to be descriptive, as witness "Scraggly Cedars," it may well be that, in times more remote than can be recalled now by the oldest natives, the Little Swash (Parkers Opening) was likewise a barren flat, and was likewise built up, by a natural process, to a lush meadow-like opening.

### The Vertebrate Fauna

Thirty-five species of tetrapod vertebrates—amphibians, reptiles, breeding land birds, and mammals—occur on the island. By comparison, more than two hundred species of the same groups breed in the Coastal Plain of North Carolina. The lists of species present, as here given, can be regarded as reasonably complete. With few exceptions, all were observed by me. Some forms have been included as a result of conversations with the natives; I have tried to be critical in this respect. Names of species included on this basis are enclosed in brackets.

Lists are given also of those forms thought probably (or definitely or almost certainly) to be absent from the fauna. The "probably absent" lists, because they aid in drawing a more nearly complete faunal picture, are a desirable addition to faunal data. In this paper, the species or groups of species on such lists represent some of those known to occur on the mainland or on adjacent islands but not found by me on Ocracoke. Not all of the species expected to be present on the island were listed as "probably absent" if not found; none was placed in this category without careful consideration from each of several obviously pertinent points of view, as follows:

(1) A few species are narrowly limited with regard to habitat; when the habitat is also limited to very small areas, thorough search of the habitat is possible in a relatively short time. If under these conditions diligent search fails to turn up specimens, one can be reasonably certain of the absence of the species in question (for example, *Gastrophryne*, in decaying wood of logs and stumps).

(2) Some types of habitats, necessary for certain species, may be entirely absent (lack of permanent fresh-water pools, correlated with absence of such amphibians as *Rana clamitans*, with a larval life longer than one season in duration).

(3) Certain species when present in a given area are so conspicuous because of their habits, that they could hardly be missed in diligent observation, even in a comparatively short time (night voice of Chuck-will's-widow, surface runs of moles).

(4) Some species are so conspicuous that their presence could not be unknown to men habitually as close to nature as are the natives of these islands (larger mammals, such as bear, skunk, fox, etc.; or brilliant birds, such as

the cardinal, painted bunting, etc.; or poisonous snakes, such as the rattlers).

Only when rigorous inspection of all observable or obtainable facts indicates that a species can be excluded, without reasonable doubt, on the basis of one or more of the above viewpoints, is it placed on the "probably absent" list. In general, those species which could be expected to occur but which were not found, and which after consideration of the foregoing points could not definitely be classified even as "probably" absent, are species of secretive habits and low population numbers, such as most snakes and a few birds. These undoubtedly will account for any degree of incompleteness the "species present" lists may prove to have. It may be pertinent here to note that with the exception of two of the snakes, each of the species found on the island was observed in both seasons of field work; the green snake was seen in the first season only, and the king snake only in the second.

Terminology in these lists follows standard American authorities, as follows: for amphibians and reptiles, Stejneger and Barbour (1933); for birds, American Ornithologists Union (1931); for mammals, Miller (1924). Common names as used by the natives of Ocracoke Island are placed in quotation marks.

#### AMPHIBIA

##### Present:

*Bufo fowleri*. Fowler's toad; "toad-frog."

? [*Hyla* (squirrela?)]. Southern tree-frog; "spring frog"; (recently exterminated?).

##### Probably absent:

*Urodela*. Salamanders.

*Bufo quercicus*. Oak-toad.

*Rana* spp. True frogs.

*Gastrophryne carolinensis*. Narrow-mouthed toad.

Fowler's toads are quite common; they were found in all the habitats except true salt marsh. Not frequently met with in the daytime, they were most readily observed and collected after dark, during a rain. Their chorus was heard almost every night during our stay. No tree-frogs were seen; the species is recorded on the basis of natives' description of a small agile, green "spring-frog," sometimes found in their cisterns, and with startling saltatorial powers (cf. page 297).

#### REPTILIA

##### Present:

*Ophisaurus ventralis*. "Glass-snake."

*Cnemidophorus sexlineatus*. Swift; "sand lizard."

*Opheodrys aestivus*. Rough green snake; "green snake."

*Coluber constrictor*. "Black snake"; "horse-racer."

*Lampropeltis getulus*. King-snake.

*Natrix sipedon*. Banded water-snake; "water-mocassin."

*Kinosternon subrubrum*. Mud-turtle; "hickity."  
*Chelydra serpentina*. Common snapper; "swamp-turtle."  
*Clemmys guttata*. Spotted turtle; "highland hickity."  
*Malaclemys centrata*. "Diamond-backed terrapin."

Probably absent:

*Alligator mississippiensis*. Alligator.  
*Anolis carolinensis*. Green lizard or Carolina "chameleon."  
*Eumeces fasciatus*. Blue-tailed skink.  
*Agkistrodon* spp. Moccasins.  
*Crotalus* spp. Rattlesnakes.

The swifts and the several turtles make up the bulk of the reptilian population. Swifts are very common, chiefly about the thickets scattered in the sea oats. It was not rare to stumble onto a half-dozen mud-turtles during a morning's walk, or a similar number of spotted turtles. Terrapin are numerous enough to form a staple in the natives' diet. One glass-snake was seen each year; one in rank growth of grasses and shrubs beside the Knoll Oaks, and one on the edge of Molasses Creek Opening. Snakes were seldom seen, except the banded water-snake, which was abundant in the tidal creeks. The single green snake was found in the spike-rush marsh (*Juncus*) about 30 feet from a clump of marsh elder (*Iva*), the nearest shrubs (1940, not seen in 1941). The black snake was met twice each year, among the sea oats, near thickets and in dry grasses of the swash. The king snake was taken close by camp in 1941; it is strikingly different from typical *getulus* in color (chocolate brown), in pattern of coloration on the head, and in the arrangement of rings; it may represent a distinct, hitherto undefined, insular race.

#### AVES<sup>5</sup>

Present:

*Cathartes aura septentrionalis*. Turkey vulture; "buzzard"; (casual).  
 \**Zenaidura macroura*. Mourning dove.  
*Coccyzus (americanus?)*. Cuckoo; "rain crow."  
*Colaptes auratus*. Flicker; "woodpecker"; (casual?).  
 †*Tyrannus tyrannus*. Kingbird.  
 \**Myiarchus crinitus*. Crested flycatcher.  
 \**Hirundo erythrogaster*. Barn swallow.  
 \**Corvus ossifragus*. Fish crow.  
 †*Thryothorus ludovicianus*. Carolina wren.  
 \**Mimus polyglottos*. Mockingbird.  
*Toxostoma rufum*. Brown thrasher.  
 \**Dendroica discolor*. Prairie warbler.  
 \**Geothlypis trichas typhicola*. Yellow-throat.

<sup>5</sup> Exclusive of shore- and aquatic birds.

\* Nests with eggs or nestlings, or fledgling birds, observed by me.

† Other evidence of breeding observed (e.g., edematous broodpatch of females, enlarged testes of males).

- \**Passer domesticus*. English sparrow.
- \**Sturnella magna*. Meadowlark; "fieldlark."
- \**Agelaius phoeniceus*. Red-wing; "jack"; "jackdaw."
- \**Cassidix mexicanus*. Boat-tailed grackle; "blackbird."
- \**Ammospiza maritima macgillivraii*. Seaside sparrow.
- \**Melospiza melodia atlantica*. Song sparrow.

Probably absent:

- Antrostomus carolinensis*. Chuck-will's-widow.
- Chordeiles minor*. Nighthawk; "bull bat."
- Chaetura pelagica*. Chimney swift.
- Piciformes*. Woodpeckers (except flickers?).
- Passerina ciris*. Painted bunting.
- Pipilo erythrophthalmus*. Towhee.

Vultures were seen soaring over the island on three different days, always on a northerly wind; they probably do not breed on Ocracoke. A single pair of flickers was seen, in 1940, foraging on the margin of the Great Swash; one collected was an immature bird, the other made off to the Knoll Cedars and was not seen again, although looked for repeatedly. Natives say that "woodpeckers" are abundant in winter. A brown thrasher was seen and heard on two different days in the marginal thickets near Quarks Point, in 1940; a pair was seen at the Hammock Oaks in 1941. A cuckoo was heard twice at the Hammock Oaks in 1940, and once again at the same place in 1941.

The remaining fifteen species were all very common, each seen or heard in numbers every day both years. Besides the gregarious and conspicuous boat-tailed grackles, fish crows and red-winged blackbirds, the abundant and widely distributed birds are those of the thickets—mockingbird, song sparrow, Carolina wren, prairie warbler and yellow-throat. Meadowlarks are numerous on the swashes and openings; mourning doves, also common, range chiefly over the marginal thickets and sea oats. Seaside sparrows were found only in the *Juncus* marshes, and crested flycatchers only about the small patches of woodland. Kingbirds were least abundant of the common birds.

The English sparrow seems to be confined to the vicinity of the community, where it is abundant; none was observed anywhere between the Plains and the Great Swash. The barn swallow likewise was confined to the general neighborhood of buildings but not restricted to the community; a pair nested in the woodshed at Dick's Camp in 1940 and again in 1941; another pair was nesting in an abandoned shack near the Hammock in 1940.

#### MAMMALIA

Present:

- [*Mustela vison mink*]. Mink.
- Rattus rattus*. Black rat.
- Mus musculus*. House mouse.
- Sylvilagus palustris*. Marsh rabbit; "cottontail."
- Sylvilagus floridanus*. "Cottontail."

Probably absent:

*Didelphis virginiana*. Opossum.

*Insectivora*. Moles and shrews.

? *Chiroptera*. Bats.

*Carnivora*. (Except mink, occasional otter.)

*Sciuridae*. Squirrels and chipmunks.

*Cricetidae*. Native rats and mice (except *Oryzomys*?).

*Odocoileus virginiana*. Deer.

The mammalian fauna is decidedly poor, especially in native species. The marsh rabbit and the cottontail are fairly abundant. Rice rats (*Oryzomys*) may occur on the island although none was obtained in extensive trapping either along the marginal thickets or the duneward edge of the marsh, where rice rats are known to occur on other islands. Quite certainly, there are no other native American mammals, if we except occasional mink and otter. This is especially striking in view of the known occurrence of the opossum, mole, raccoon, muskrat, meadow mouse and white-footed mouse on neighboring Hatteras Island.

There were some house rats in the outbuildings at Dick's Camp. Mr. O'Neal says they are numerous in winter, but he thinks they move out into the marshes in summer. A black rat was taken in a live-trap baited with rolled oats, set in the marginal yaupon thicket within a few yards of the sea oats on the inner border of the Great Swash.

House mice are numerous, and the population is highly variable in color pattern. Twenty three mice were taken in 150 trap-nights in the sea oats and dune thickets. Of these, only three had the grayish belly typical of the mainland house mouse. The remaining twenty all had white underparts, either pure white bellies with a distinct buffy-yellow pectoral spot or white bellies with the tips of all hairs buffy yellow. There seemed to be no age differences in this respect. Two of these mice showed a distinct white forehead blaze, and three more had at least a few white hairs on the forehead.

It is generally agreed that bands of wild ponies roamed along the entire outer banks of North Carolina more than two hundred years ago; and it is assumed that these were descendants of ponies escaped from some early Spanish ship. There is as yet no evidence that they were simply liberated by early settlers; apparently their invasion of the islands preceded that of man. The Ocracoke ponies are no longer "pure," since a wealthy sportsman recently persuaded the owners to castrate all stallions and permit the mares to breed with his polo pony, with the intention of improving the stock. The Ocracoke band still freely roams the island in a semi-feral state.

#### RECENT CHANGES IN THE FAUNA

There are no available references to the wildlife of early days, and only meager information is available from the older residents. Of this information, the most tangible and positive concerns a few thicket-woodland birds. Catbirds

(*Dumetella*), which I did not find, and brown thrashers (*Toxostoma*), of which I saw only two, are both said to have been very common relatively recently (1890-1900). Another bird supposed to have been not uncommon was called the "hanging bird," which from the description of its nest I judge was an oriole (*Icterus*). The natives seem to be familiar with the cardinal (*Richmondia*), and say that a few years ago a pair nested in the village; but no one could say that this species had ever been numerous on the island.

I was also told that there "used to be" many bats, and certainly the older men talked very familiarly of them; but although I watched for them every evening during both summers, I saw none, nor did any of the men say that bats had been seen on the island recently.

The small, green "spring-frog" (*Hyla?* sp.) described to me by the islanders may also have disappeared in the past few years. In the spring of 1941, I offered the boys of the island a fancy price for some of these, but seemingly none was to be found. In the preceding five years there had been at least two extended periods of drought, during which all of the cisterns on the island had gone completely dry. If, as had been indicated, the "spring-frog" was confined to this habitat, the species might not have been able to survive a series of such adverse periods.

Arguments are offered below for the former occurrence of moles (*Scalopus*) and white-footed mice (*Peromyscus*) on that section of the island above Styrons Hills, from which they must have disappeared sometime during the past fifty to one hundred years. Neither species probably ever inhabited the section below the Tar Hole Beach.

### Ecological Distribution of Vertebrates

*Beach* (barren upper beach and areas of sparse "beach vegetation"). This habitat is essentially devoid of terrestrial vertebrate life, although barn swallows and fish crows, besides some semi-aquatic birds, are often seen flying over, and fish crows sometimes forage here. In the very few instances in which beach vegetation is adjacent to dry thickets (Ocracoke village, soundward side chiefly; Fig. 6, lower) *Cnemidophorus* wanders out into this habitat. About thirty Least Terns were nesting on the barren beach opposite Molasses Creek Opening in 1940.

*Dune* (the *Uniola-Yucca* association; Fig. 3; Fig. 4, lower). Mourning doves and meadow larks forage here; *Cnemidophorus* occurs regularly, but is most abundant in and about dry thickets. Mocking birds and song sparrows also forage here, but only in the immediate neighborhood of thickets. House mice are numerous and both species of rabbits forage here in early morning.

*Dune thickets* (usually wax myrtle or southern prickly ash, only occasionally yaupon-holly; low brush, one to four feet in height, in patches covering up to several square yards; sea oats, yucca and cactus between the patches, surface of ground dry; Fig. 4, upper). This is the favorite habitat of *Cnemi-*



*dophorus*; mockingbirds, song sparrows, and house mice are abundant; Fowler's toad sometimes occurs.

*Marginal thickets and woods* (thicket woodland; between dune-dune thicket area and salt marsh; thickets, chiefly yaupon-holly; woods, live oak and red cedar, occasionally red bay; ground surface dry, sandy, to slightly moist, more humus; Figs. 5-6). Fish crows and boat-tailed grackles roost and nest in the trees and taller thickets; crested flycatchers nest in the hollows of live oaks; prairie warblers and kingbirds are not uncommon. Yellow-throats, Carolina wrens and Fowler's toads occur occasionally; mockingbirds, song sparrows and *Cnemidophorus* only about the margins. Rabbits find shelter here; house mice occur, but less commonly than in the previous two habitats.

*Marsh thickets* (some wax myrtle, but chiefly yaupon-holly, within the marsh; taller than the dune thickets, reaching to fifteen feet or higher; soil always moist to wet; beneath and between yaupon a rank growth of grasses and rushes; Fig. 8). Fowler's toad is more common here than elsewhere; the lizards (*Cnemidophorus*) do not venture down from the dry thickets above. Carolina wren and yellow-throat here reach their greatest abundance. Other birds of dune thickets and marginal thickets occur here also; kingbird and crested flycatcher are found where the thickets are extensive. In the tallest thickets, boat-tailed grackles nest; red-winged blackbirds are usually associated with the grackles.

*Salt marsh* (*Juncus*; Fig. 7, lower). Only the seaside sparrow was found here, and it was never seen outside the dense stands of spike rush; various other birds fly over this habitat. (See also *aquatic-brackish*.)

*Swashes and openings* (meadow-like; thick cover of shorter grasses, sedges etc.; Fig. 7, upper). Meadowlarks are most prominent but mourning doves are not uncommon; both nested in this habitat. Fowler's toad, mud-turtle, and black snake wander about on the swash.

*Aquatic, fresh* (small, temporary or temporarily fresh-water pools, scattered through the thicket-woodland, occasionally about marsh-thickets; temporary, very shallow pools on the "openings," especially the Great Swash, conspicuous after heavy rainfalls). Spotted turtles and mud turtles are common in these pools, but the former seems not to go out into the openings and swashes. Fowler's toad breeds in such pools (tadpoles were found in several) but the adults are not more abundant about these waterholes than elsewhere (at least in late June and early July).

*Aquatic, brackish* (tidal creeks and salt-marsh ponds and pools). Two reptiles, the diamond-backed terrapin and the banded water-snake, are abundant in this habitat. Terrapin were seldom seen outside of these waters and then only in the short salt grasses usual about the pools and the creek mouths. At the heads of these creeks, small pits usually have been eroded, and in the pools so formed both spotted turtles and mud-turtles are found, the latter very commonly. The only snapping turtles seen were in such pools. *Natrix* occurs here also, but terrapin were not observed. The water at the heads of these



creeks and in these pools may be very nearly fresh, especially after heavy rains on southerly winds.

*Edificarian* (in addition to the buildings of the village, isolated and abandoned shacks scattered along the duneside margin of the thicket-woodland: several between the Plains and the Great Swash; several large abandoned erosion control crew barracks, besides Dick's Camp, at the Knoll. Two birds and two non-native rodents are to be placed here, the English sparrow, barn swallow, black rat and house mouse. The sparrow is limited to the village; the barn swallow nests even in isolated buildings far from human habitations; the occurrence of the two rodents in buildings probably is conditioned as much by food supply as by shelter.

### Discussions and Conclusions

No species of vertebrate occurring on Ocracoke is absent from the mainland, but more than 80 per cent of the mainland species do not appear in the Ocracoke fauna. This impoverishment is due to several factors, the effect of each of which varies according to the species concerned. The degree of accessibility of an area limits the number of species capable of invading it, while its geographical relationship to "faunal areas" determines the precise kinds available for invasion. The actual establishment of a species following invasion of individuals is then conditioned by the presence of suitable habitat and by the size (total area) of the habitat—a factor of "suitability" of habitat which deserves emphasis when the consideration is for the species, not merely for individuals, because the habitat must be large enough to support a breeding population of sufficient size to insure the maintenance of the species. Finally the maintenance of the species following establishment depends on the continuance of favorable habitat conditions. These are statements of principles probably applicable to any area at any time; each finds illustration in the analysis of the Ocracoke fauna.

The relative accessibility of offshore bars varies with their age. The young bars, formed at some distance from the mainland, are accessible only to such forms as can cross the intervening salt water barrier. These species would be of three types: those that fly, those that swim, and such others as could withstand the rigors of transport on drift over salt water. The first group includes birds and bats; the second, turtles, some snakes and especially *Natrix*, and probably some mammals, such as mink, otter, muskrat, and perhaps rice rats. The third group would include any form which because of its habits might sometimes be caught up by flood waters or otherwise find itself accidentally adrift in a current.

In the course of development, however, the offshore bars are pushed back toward the coast, the fully mature bar finally coming to rest against the mainland. It is to be doubted that the Carolina outer banks ever attained this stage of development, although their present great distance from the mainland is chiefly the result of submergence of the coast and drowning of the river valleys, as shown by the deep embayments of the Neuse and Pamlico Rivers.

At the upper, northern end of the series, however, they are tied in to the mainland at Cape Henry; and it is highly probable that they were formerly also united to the mainland at the southern end through Bogue Banks. Here, then, is a direct land way of ingress, from the mainland to each end of the series of islands. This establishes the possibility of eventual invasion, along a land way, of all the islands in the chain, since adjacent islands may be periodically united and again separated, by the closing and later reopening of an inlet.

This latter phenomenon, part of Johnson's (1919) theory of development of offshore bars, is illustrated by the history of Hatteras Inlet, discussed above, which shows that Ocracoke for at least one lengthy period was continuous with Hatteras, and that indeed a part of Hatteras island (present Hatteras Inlet to Styrons Hills) has been transferred to Ocracoke. That the necessarily simultaneous transfer of fauna from Hatteras to Ocracoke did not however permanently contribute to the facies of the Ocracoke fauna is emphasized by the great difference in their mammalian fauna, specifically the paucity of that on Ocracoke (cf. page 296).

Moles (*Scalopus*) were expected between Styrons Hills and Hatteras Inlet, the area which was, up to 1846, a part of Hatteras Island, where moles are now abundant. The habitat (Fig. 9) seems to be entirely suitable, being essentially similar to much of Hatteras Island inhabited by moles. Two possible explanations for their absence present themselves. Since the Hatteras population has probably moved down the banks from above, maybe from Cape Henry, perhaps it had not reached, by 1846, the point at which the bar was then breached to form the present Hatteras Inlet. An alternative explanation would assume that the moles had reached Styrons Hills, and that the Ocracoke population, sometime after its sudden isolation on September 7, 1846, was drowned out by one or more of those periodic, violent storms during which all this section except the higher dunes would be inundated.

The latter possibility seems to me the more likely. It might be contended that the absence of moles from the rest of Ocracoke Island, below Styrons Hills, indicates that moles had not reached Hatteras Inlet by 1846, since it will be remembered that the old Hatteras Inlet closed up about 1750, forming a continuous land way from Hatteras to Ocracoke Inlet, and giving ample time for dispersal. The idea and even the expression "land way" is however misleading. The Tar Hole Beach is and seemingly always has been a barren flat (cf. Fig. 10); and it could not be passed by small animals in the normal manner of passive dispersal and extension of range. It is frequently flooded by high tides, especially in winter, and offers neither food nor shelter. Individuals would have to cross it in one leap, an entirely unlikely migration for animals whose territory and home range is to be measured at most in hundreds of feet, not in hundreds of yards. A barren flat like the Tar Hole Beach is probably as effective a barrier for small animals as an inlet or other stretch of water.

When the new inlet was opened, in 1846, the Great Swash also was a barren flat, overflowed by some tides, exactly as is the Tar Hole Beach today, and up to about 1890 it provided a second barrier to the southward extension of small land animals. If, before 1846, both the Tar Hole Beach and the Great Swash had been covered by vegetation, such as grew up over the latter some fifty years later, then undoubtedly the moles could have extended their range gradually into and through the central part of the island. Here, around the Knoll and the Six-mile Hammock, they might have found sufficient shelter from the occasional hurricane floods to preserve a breeding population. But, such vegetation being absent, the barren flats prevented the extension of range below Styrons Hills, and held in this area an isolated and necessarily small population, without shelter and protection from floods, the new inlet after 1846 barring reinforcement from the numerically healthy Hatteras population.

In 1846, white-footed mice (*Peromyscus*) also undoubtedly inhabited the area immediately above Styrons Hills. They occur now in the woods about and below Cape Hatteras, a habitat which formerly extended from here southward to Styrons Hills (Price, 1795), which existed on the site of the present Hatteras Inlet when it was cut in 1846 (Welch, 1885), and which did not disappear until quite recently. The older men now living on the island recall that as small boys they frequently picked grapes in a thick growth of "scrub" and "cedars" around the Hatteras Inlet Coast Guard Station, between Styrons Hills and Hatteras Inlet. The disappearance of this habitat (1890-1900) would have resulted in the disappearance of the white-footed mice; meanwhile, like the moles, they had been prevented from moving on down the island, where they might have found suitable conditions, by the broad, barren stretches of the Tar Hole Beach and the Great Swash.

Lateral migration along the bars over a continuous land way thus is not made possible simply by the closing of inlets or the transfer of land through a combination of the closing of one inlet and the creation of another. It depends also on the subsequent maintenance of suitable habitats; but the very physiographical and meteorological factors responsible for the closing and opening of inlets are those which act destructively on all vegetational habitats, except possibly marsh and dune grassland. Lateral migration depends on the growing up of suitable habitats also over the emerged inlets, and probably only dune and marsh grassland types could be dispersed along such routes. Thus moles might have made their way over the Tar Hole Beach if this had become covered with grasses, as the Great Swash did become covered forty years ago; but it and the Great Swash would have remained still an ecological barrier for the white-footed mouse, a thicket-woodland form.

For the larger, more mobile animals with greater cruising ranges (opossum, deer) the emerged inlet, with or without vegetational cover, might provide a land way for the migration of individuals into a new and unoccupied habitat. Such migration depends obviously on the occurrence of suitable habitat, in this case woodland, in the newly accessible area; but the presence of woodland in itself is not enough, it must be of sufficient size to maintain a permanent

breeding population. The absence of extensive woodland on Ocracoke, then, most likely accounts for the absence from it of opossum, raccoon and deer, despite the one-time existence of a land way over which they might have come from Hatteras. Deer and raccoon are known to have inhabited Hatteras at least since early post-Columbian times, and opossum at least as far back as the memory of oldest living natives.

Both the painted bunting (*Passerina ciris*) and the Carolina "chameleon" (*Anolis carolinensis*), absent from Ocracoke despite the presence of seemingly suitable habitat, occur on Shackleford Banks and Harkers Island and on their adjacent mainland. Contrarily, song sparrows (*Melospiza melodia*), which are abundant on Ocracoke, do not range that far southward. These data suggest that there exists, somewhere just below Ocracoke, one of those intangible barriers that marks off so-called "faunal areas"; and this also contributes to the delimitation of the Ocracoke fauna.

The great restriction of the amphibian fauna is related probably in large measure to the total absence of permanent fresh-water pools and to the frequent salting of such shallow temporary pools as do exist through flooding from the sea. The continued existence of the small tree-frog, if indeed it has not already been exterminated by droughts, probably is conditioned by the islanders' habit of storing rain water in large cisterns. This leaves *Bufo fowleri* as the single amphibian successful in firmly establishing itself here under natural conditions. That individuals of other species might have reached Ocracoke without succeeding in maintaining themselves is indicated by comparison with other islands of this region. Thus, Harkers Island, in Back Sound, harbors eight species of six families of amphibians; on Shackleford Banks are five species representing five families.

The relative paucity of breeding species of land birds reflects the almost complete absence of woodland forms, which can be related to the small total area, and lack of variety, of woodland on the island. There are no pines, no oaks except the live oak; there are, in fact, only three trees: a few small patches of live oaks, only an occasional red cedar, and a very few red bays. Testimony of the older natives as to the former abundance of catbirds and brown thrashers, and their present scarcity, may be correlated with recent diminution in extent of the wooded areas; but an early colonial description (Price, 1795), quoted above, is evidence that the woodland never was extensive.

The absence of trees other than the three mentioned carries with it the absence of stubs and logs with loose bark and soft, pulpy wood (such as is furnished by pine), which is the favorite habitat of blue-tailed skinks (*Eumeces fasciatus*) and narrow-mouthed toads (*Gastrophryne carolinensis*). Skinks have frequently been observed under loose bark of live oak on other islands; their apparent absence from Ocracoke then might be correlated with the limited number of such trees, or with the absence of breeding places such as furnished by logs of other types.

Man has played a significant role in determining the invasion, establishment and maintenance of other faunal elements. It seems most probable that some species reached the island either directly or indirectly through him; these are the house mice, the rats, and the now only semi-feral banks pony. It is also possible that he brought the amphibians. At least two more species, the English sparrow and the barn swallow, were able to establish themselves only because he had created a habitat suitable for them which the area otherwise would lack. The house mouse and banks pony have demonstrated elsewhere (Shackleford Banks) that they are independent of man and his structures for their maintenance, once they have been introduced and established; but should he abandon Ocracoke Island, as he did abandon Shackleford Banks about 1910, then two species, at least, the English sparrow and the barn swallow, almost certainly soon would be eliminated from the fauna.

### Summary

The North Carolina "outer banks" are offshore bars, submarine in origin; the present flora and fauna therefore was acquired sometime subsequent to the emergence of the bars. A study of the vertebrate fauna has been undertaken to determine which species have become established on the islands and to analyze the several factors concerned, namely, source of invading species, possible routes of invasion, kinds of invading species, limiting factors in establishment and maintenance of invading species, and degree of differentiation attained, if any.

Of these bars, Ocracoke Island is probably now the most nearly inaccessible to invading species. Its exposed position subjects it to periodical violent storms, during which most of the island is inundated, and as a result of which the populations are periodically decimated, and the topography and habitats made unstable. From about 1750, when old Hatteras Inlet closed up, until 1846, when the present Hatteras Inlet was formed, Ocracoke was continuous with Hatteras Island. The new inlet was cut through the bar about five miles northeastward of the former inlet; thus the northeast portion of Ocracoke Island was originally part of Hatteras Island. Except for an irregular line of dunes fronting the sea, the island is almost entirely less than three feet above sea level. The strand is barren, the sand dunes covered with a characteristic grass, "sea oats." Dry thickets are scattered on the inner side of the dunes; back of this area a line of thickets borders the salt marsh, which extends to the shore of the sound; there are only a few small patches of woodland.

On this island are found a single amphibian, two species of lizards, at least four snakes, four turtles, seventeen breeding species of land birds, and five or possibly six mammals, two of which are non-native. These make up only about 17% of the total number of species in the fauna of the adjacent mainland. Of species or groups of species found on adjacent islands or mainland, the following probably are missing from Ocracoke: urodeles, *Rana*; *Alligator*, *Anolis* and *Eumeces*; crotaline snakes; nighthawks, swifts, hummingbirds,

woodpeckers, titmice and nuthatches; moles, shrews, squirrels, and native rats and mice. The meagerness of the fauna is ascribed to several factors: relative inaccessibility; geographical relationship to "faunal areas"; absence of certain habitats and small size (total area) of others; and relative instability of favorable habitat conditions. The factor first mentioned limits the number of animals capable of invading the island, while the second determines the precise kinds available for invasion. The third factor limits the establishment of invading species; the last-mentioned factor reduces the certainty of maintenance of species following establishment. The one-time merger of Ocracoke with Hatteras Island and subsequent transfer to the former of part of the latter had little effect if any on the faunas of the Ocracoke fauna, as evidenced especially by the absence of several species of mammals now occurring on Hatteras. At least four members of the fauna (roughly twelve per cent) owe their presence on the island to man; of these, one species certainly, and probably a second, are now independent of him, but at least two established species could not maintain themselves there, if he should abandon the island, because of the resultant loss of the edificarian habitat on which they depend.

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## A List of the Fishes of the Mainland of North and Middle America Recorded from both Freshwater and Sea Water

Gordon Gunter

The relation of coastal fishes to salinity of the environment is one of the most important aspects of their natural history. The whole problem, because of its connections with physiology and ecology, has bearing on one of the oldest and most important steps of biological evolution, the migration of animals from sea to land. In this paper one aspect of this many-sided problem is examined, by taking the step of compiling a list of fishes of the continent of North and Middle America that have been found in both freshwater and sea water.

Attempts have been made to classify all aquatic animals as euryhalin, those that can withstand relatively large changes of salinity of the water, or stenohalin, those that cannot withstand such changes. This is impossible for such a distinction is not sharp in nature. Between the two large groups of fishes that are confined to either freshwater or sea water, there are species with varying degrees of tolerance to both mediums. The terms euryhalin and stenohalin have never been rigorously defined. This is understandable, for the nature of the concept is such that a rigorous definition would be arbitrary. Nevertheless, a rigorous definition may be of use when the relative euryhalinity and stenohalinity of various fishes are compared under rigid experimental conditions. According to Keys (1933), the eel, *Anguilla*, is better able to tolerate salinity changes than the salmon, the stickleback, *Gasterosteus*, and some of the Cyprinodontidae, all fishes ordinarily considered to be euryhalin. Summer (1911) has shown that most specimens of *Fundulus heteroclitus* will succumb after a time when transferred abruptly from sea water to freshwater. Yet the fish is found in nature in both habitats, as is well known, and is considered to be a good example of a euryhalin species. Abrupt transfers from one environment to the other are not the rule in nature.

For the present purpose a euryhalin fish will be defined as one which can transfer from sea water to freshwater or the reverse, under natural conditions; and as evidence of this ability records of a species from both environments, made by competent observers under natural conditions, will be acceptable.

I am inclined to believe that fishes which cannot withstand freshwater veer away from it and are seldom accidental strays into rivers, at least not often enough for the uncommon ichthyological collector to record them. However, certain marine fishes on the list that follows may not be able to remain indefinitely in freshwater. Of this we have no way of telling without experimentation. Quigley (1928) has shown that the heart of *Squalis suckleyi*, one of the

clasmobranchs on the list, stops beating about two hours and twenty-five minutes after the animal is transferred to freshwater. On the other hand, I have called attention before (1938b) to the fact that the Tarpon, *Tarpon atlanticus* (Cuvier and Valenciennes), and the Broad Sole, *Trinectes maculatus* (Bloch and Schneider), have been known to live indefinitely in freshwater. I know of no experiments on the two species and the transfers from sea water may or may not have been abrupt. It has been stated that certain freshwater fishes must return to their medium after having invaded the sea for a while. This is merely an assumption for little is known of the reasons for movements from one environment to the other. Conceivably, though, stenohalin fishes may venture from one environment to the other for short periods of time, for the effects of the change are not instantaneous. According to Keys (*op. cit.*), the regulatory mechanism of adaptation to salinity change only begins to work after considerable change in the osmotic pressure of the blood takes place. The time needed for such osmotic changes to take place might be equivalent to a period of grace for the stenohalin fish in the wrong environment.

Fishes that venture from freshwater to more saline water or from sea water to less saline water are very numerous. Several catostomids, cyprinids, centrarchids and other strictly freshwater fishes enter slightly salt or even strongly salt water in North America, some of them going into water that is over 12.00 parts per thousand saline (one-third sea water); witness the bay records of Hildebrand and Schroeder (1928) and Evermann and Clark (1931). A similar situation for other species farther south is shown by the various papers on Middle America. The saline limits tolerated by partly euryhalin, freshwater fishes is unknown, although one would not expect to see a *Huro*, *Archoplites* or catostomid in the open ocean. Marine fishes that come into waters that are less salty than the ocean are still more numerous, and fishes that live or spend part of their time in waters that are neither fresh nor fully marine make up a sizeable percentage of the fishes of North America. The same situation probably applies to the whole earth.

Probably most freshwater fishes can be accustomed to low concentrations of salt water. Weed (1925) has recorded several marine and freshwater species from a resaca near Brownsville, Texas, all apparently in good condition, although the salinity (undetermined) was, as he stated, so high that a swimmer had difficulty in touching bottom in five feet of water. Even *Polyodon spathula* (Walbaum), which is considered to be a purely freshwater fish (Myers, 1938), goes into brackish water. The writer took one in January, 1933, in Lake Ponchartrain (salinity undetermined) in company with Croakers, *Micropogon undulatus* (Linnaeus), Spots, *Leiostomus xanthurus* Lacépède, Blue Crabs, *Callinectes sapidus* Rathbun, and other marine animals.

Some fishes enter bays and estuaries when the salinity is high and leave immediately for the open sea when it falls. Certain marine fishes may go into freshwater only once a year. Others, such as *Mugil cephalus* Linnaeus, the Striped Mullet, probably come and go several times a year. Some may be rare visitors in freshwater. They are included indiscriminately on the list without



attempts to separate them, for this is an impossible task at the present stage of knowledge. The same statement applies to the freshwater fishes in the sea.

The method of compiling the list was simple. Check lists were used. These are relatively unsatisfactory and I have consulted and checked, by correspondence chiefly, with many authorities on the various parts of the continent. Most of them have shown an interest in the problem and some have given an extraordinary amount of cooperation. Each questionable record has been rechecked. In some instances the exact locality record was not given. In such cases I have had faith in the correctness of my informant's information. It is believed that the list is conservative and that as time goes on data adding more species to it will be forthcoming. In instances where there were indications that a certain fish belonged on the list, but no clear-cut records could be found, it was placed in what is called the Probably Euryhalin group.

The authority for the inclusion of most species is given. In some cases it is not necessary for the characteristics of the species are common knowledge. Many of the references may or do cite the first authority recording a species in fresh or salt water, but priority was not followed and many citations are merely to a good record or authority. When a fish is commonly known to live in one environment, the work cited generally gives proof of its existence in the other.

By each species a capital letter is placed to indicate the grouping of the fish; whether anadromous, catadromous, freshwater or marine. In this grouping family affinity was followed as nearly as possible. For instance, all gobies are called marine although some of them inhabit freshwater. In such instances the environmental affinity of the species is noted by a letter in parentheses, following the first letter. The term anadromous cannot be applied with sharp distinction. The Brook Trout, *Salvelinus fontinalis* (Mitchill), has a sea run form and I am classing the species with other salmonids in calling it anadromous. Many of the more clearly anadromous salmonids have landlocked forms and so there is a phylogenetic reason for this decision. Likewise, *Dorosoma cepedianum* (Le Sueur) is in one sense partially anadromous (Hildebrand and Schroeder, 1928; Gunter, *op. cit.*), but it is called a freshwater fish. Both *Fundulus heteroclitus* (Linnaeus) and *Microgadus tomcod* (Walbaum) ascend barely to the edge of pure freshwater at spawning time. I hesitate, however, to place them with the anadromous fishes and they are called freshwater and marine, respectively. Grouping fishes in this manner can only be done arbitrarily and it is possible that ichthyologists will not agree in some cases. Such disagreements, however, will not be numerous enough to affect the conclusions given later in the paper.

The four geographical divisions of the list are self-explanatory. They are used because they show certain results that a straight list would not bring out. The Gulf Coast of the United States is left out, for with the exception of *Alosa alabamiae* Jordan and Evermann, *Pomolobus chrysochloris* Rafinesque, and *Membras vagrans* (Goode and Bean), there is no fish there that would

not be included on other parts of the list. For the purpose of saving space, when a fish belongs on both northern and southern parts of the list, on either coast, it is listed only on the northern division, with an asterisk, and is not listed in the southern division. Subspecies are not used. Some references not seen by me are cited in the text, but not listed in the bibliography.

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**Fishes of the West Coast of North America, North of Mexico,  
Recorded from both Freshwater and Sea Water**

CYCLOSTOMI  
Petromyzonidae

*Entosphenus japonicus* (Mertens), A.—Runs up the Yukon River; Creaser and Hubbs, 1922.

*Entosphenus tridentatus* (Gairdner), A.

*Lampetra fluviatilis* (Linnaeus), A.

ELASMOBRANCHII  
Squalidae

*Squalus suckleyi* (Girard), M.—Dr. A. L. Pritchard has taken this shark in a river where the water was strictly fresh, personal communication. He added that it might have followed a school of salmon into the river. Freshwater invasion is thought to be uncommon for this shark. Quigley, 1928, has shown that the shark will live for little more than two hours when transferred abruptly to freshwater.

OSTEICHYTHES (TELEOSTOMI)  
CHONDROSTEI  
Acipenseridae

*Acipenser transmontanus* Richardson, A.

*Acipenser acutirostris* Ayres, A.

ISOSPONDYLI  
Salmonidae

*Oncorhynchus gorbuscha* (Walbaum), A.

*Oncorhynchus keta* (Walbaum), A.

*Oncorhynchus kisutch* (Walbaum), A.

*Oncorhynchus nerka* (Walbaum), A.

*Oncorhynchus tshawytscha* (Walbaum), A.

*Salmo clarkii* Richardson, A.

*Salmo gairdnerii* Richardson, A.

*Salvelinus malma* (Walbaum), A.

Osmeridae

*Osmerus dentex* Steindachner, M.—Evermann and Goldsborough, 1907.

*Hypomesus olidus* (Pallas), M(F).—Jordan and Evermann, 1898; Dr. L. P. Schultz has furnished me with several records of collections from salt water in Alaska and so has Carl L. Hubbs.

*Hypomesus pretiosus* Girard, M.—Collected from the Sandy River at Multnomah City,

Oregon, ten miles east of Portland by Dr. Carl L. Hubbs, personal communication.

*Spirinchus dilatus* Schultz and Chapman, A.

*Thaleichthys pacificus* Richardson, A.

#### Elopidae

\**Elops affinis*, M.—Glidden, 1941.

#### EVENTOGNATHI

##### Cyprinidae

*Mylocheilus caurinus* Richardson, F.—Dymond, Rep. British Columbia Comm. Fish. 1936; Prof. Dymond is of the opinion that the specimen reported here from English Bay was undoubtedly taken in normal sea water, personal communication.

#### CYPRINODONTES

##### Cyprinodontidae

*Fundulus parvipinnis* Girard, F(M).—Hubbs, 1916; Miller, 1939.

#### ACANTHOPTERYGII

##### Gasterosteidae

*Gasterosteus aculeatus* Linnaeus, M(F).

##### Atherinidae

*Atherinops affinis* Ayres, M.—Hubbs, 1916.

##### Mugilidae

\**Mugil cephalus* Linnaeus, M.—Many authors; Mr. Leo Shapovalov told me this fish sometimes gets into the Salton Sea; Dr. Hubbs wrote me that it is abundant there and is common along the Southern California coast.

##### Embioticiidae

*Cymatogaster aggregatus* Gibbons, M.—Taken in freshwater in San Luis Creek near Avila, California, May 25, 1916 by Dr. Carl L. Hubbs, personal communication; also noted in freshwater by Dr. A. L. Pritchard, personal communication.

##### Gobiidae

*Clevelandia ios* (Jordan and Gilbert), M.—Hubbs, 1916.

*Eucyclogobius newberryi* (Girard), M(F)—This freshwater goby is recorded from salt water by Hubbs, 1926.

##### Cottidae

*Leplocottus armatus* Girard, M.—Dr. Carl L. Hubbs and Dr. L. P. Schultz collected this fish in "swift and quiet fresh waters" at Rolling Beach near Seattle, Washington in 1926, and it was collected in freshwater on Admiralty Island, Alaska by Dr. Hubbs during the summer of 1939; personal communications from Dr. Hubbs.

*Astrolytes fenestralis* (Jordan and Gilbert), M.—Taken from freshwater at the mouth of a creek near Meadowdale, Washington by Dr. Hubbs, June, 1926; personal communication.

##### Pleuronectidae

*Platichthys stellatus* (Pallas), M.—Several authors; Dr. W. M. Chapman once took this fish seventy-five miles upstream in the Columbia River, personal communication.

#### Probably Euryhalin Fishes

##### OSTEICHTHYES

##### ISOSPONDYLI

##### Clupeidae

*Clupea pallasii* Cuvier and Valenciennes, M.—This fish comes to beaches to spawn and is sometimes stranded in freshwater at river mouths when the tide drops; personal communication, Dr. A. L. Pritchard.

## SYNENTOGNATHI

## Scomberesocidae

*Cololabis saira* Brevoort, M.—Pritchard, 1933.

## ACANTHOPTERYGII

## Cottidae

*Cottus asper* Richardson, F.—This fish is reported from many bays, but long search and inquiry has yielded no indubitable salt water record.

## Pleuronectidae

*Lepidopsetta bilineata* (Ayres), M.—No record of this fish beyond the possible influence of salt water has been found, but it will live for some days in freshwater aquaria, personal communication, Dr. L. P. Schultz. The fish has been taken by Dr. W. M. Chapman from the mouths of the Skagit and Quillayutte Rivers in Washington, not above possible tide effects, personal communication.

**Fishes of the West Coast of Mexico and Middle America, North of the  
Southern Boundary of Panama, that are Recorded from both  
Freshwater and Sea Water**

## ELASMOBRANCHII

## BATOIDEI

## Pristidae

*Pristis microdon* Latham, M.—Meek and Hildebrand, 1923.

## OSTEICHTHYES (TELEOSTOMI)

## ISOSPONDYLI

## Clupeidae

*Lile stolifera* (Jordan and Gilbert), M.—Dr. Carl L. Hubbs and R. R. Miller have specimens from freshwater in Rio Yaqui and Rio Mayo, Mexico, personal communication from Dr. Hubbs.

## Engraulidae

*Anchovia curta* Jordan and Gilbert, M.—Meek and Hildebrand, 1923; Hildebrand, 1939.

*Anchovia lucida* (Jordan and Gilbert), M.—Hildebrand, 1939.

*Anchovia spinifera* (Cuvier and Valenciennes), M.—Hildebrand, 1939.

## ACANTHOPTERYGII

## Syngnathidae

*Pseudophallus starkei* (Jordan and Culver) M(F)?—In the original description, Proc. Cal. Acad. Sci., V, 1895, the fish is recorded as being only in freshwater. For synonymy see Herald, 1940.

*Syngnathus elcapitanensis* Meek and Hildebrand, M(F).—This is the *S. auliscus* of Gilbert and Starks, Mem. Cal. Acad. Sci. IV, 1904, recorded from freshwater in Panama, Herald, 1940; Meek, 1908; Meek and Hildebrand, 1923.

## Mugilidae

*Mugil curema* (Cuvier and Valenciennes), M.—Evermann and Marsh, 1900, list the fish from freshwater in Puerto Rico; Hildebrand, 1939, lists it from freshwater in Panama. Dr. Kelshaw Bonham has a specimen from the Navasota River of Texas, over 200 miles from the sea.

## Centropomidae

*Centropomus armatus* Gill, M.—Hildebrand, 1925.

*Centropomus nigrescens* Günther, M.—Hildebrand, 1925; Meek and Hildebrand, 1925.

*Centropomus pectinatus* Poey, M.—Meek, 1914; Hildebrand, 1925.

*Centropomus robalito* Jordan and Gilbert, M.—Jordan and Evermann, 1900; Meek, 1914; Hildebrand, 1925.

## Lutianidae

*Lutianus argentiventris* (Peters), M.—Meek, 1907, 1914.

*Lutianus colorado* Jordan and Gilbert, M.—Hildebrand, 1939.

*Lutianus novemfasciatus* (Gill), M.—Hildebrand, 1925, 1939.

## Gerridae

*Gerras brevimanus* Günther, M.—Meek, 1914; Meek and Hildebrand, 1925.

*Gerres cinereus* (Walbaum), M.—various authors; Evermann and Marsh, 1900.

*Eucinostomus californiensis* (Gill), M.—Jordan and Evermann, 1900; Meek, 1914.

*Diapterus peruvianus* (Cuvier and Valenciennes), M.—Meek, 1907.

*Diapterus lineatus* (Humboldt and Valenciennes), M.—Meek and Hildebrand, 1925, give an account of two specimens, taken, but not by them, in freshwater in Lake Acapulco.

## Otolithidae

*Cynoscion albus* (Günther), M.—Hildebrand, 1939.

## Eleotridae

*Dormitor latifrons* (Richardson), M(F).—Meek, 1914, Meek and Hildebrand, 1916, 1923, record this species as being from the Pacific Coast and rivers. According to Meek, species of this genus return to the sea.

*Gobiomorus maculatus* (Günther), M(F).—This fish is included in lists of marine fishes, although it is generally taken in brackish or freshwater. Meek, 1914, says fishes of this genus return to the sea.

## Gobiidae

*Gobionellus sagittula* (Günther), M.—According to Jordan and Evermann, 1900, this fish is common in rivers. It was recorded from Rio Mulege, Mexico by Ginsburg, 1932, although he did not make the collection.

## Carangidae

*Caranx hippos* (Linnaeus), M.—Ascends streams on the Pacific coast, Meek and Hildebrand, 1925; Dr. A. F. Carr, Jr., has furnished notes recording this species from freshwater in Homosassa Springs, Florida.

## Tetradontidae

*Sphoeroides annulatus* (Jenyns), M.—Meek and Hildebrand, 1925.

*Canthigaster punctatissimus* (Günther), M.—Meek, 1908, Notes on Freshwater Fishes of Mexico and Central America, records this species from Isle de Coco.

## Bothidae

*Citharichthys gilberti* Jenkins and Everman, M.—The freshwater phase of this fish was thought to be a new species by Jordan and Goss, 1889.

## Achiridae

*Achirus fonsecensis* Günther, M.—Meek, 1904, 1914; Meek and Hildebrand, 1928.

*Achirus mazatlanus* (Steindachner), M.—Jordan and Evermann, 1900; Meek, 1904; Hildebrand, 1925; Meek and Hildebrand, 1928.

Probably Euryhalin Fishes  
OSTEICHTHYES (TELEOSTOMI)

## ISOSPONDYLI

## Clupeidae

*Sardinella stolidifera* (Jordan and Gilbert), M.—Taken in tide streams, Meek and Hildebrand, 1923.

## NEMATOGNATHI

## Ariidae

*Selenaspis dowii* (Gill), M.—Ascends streams, Meek and Hildebrand, 1923.

*Galeichthys guatemalensis* (Günther), M?—Hildebrand, 1925.

*Galeichthys seemani* (Günther), M.—Ascends streams to brackish water, Meek and Hildebrand, 1923.

SYNENTOGNATHI  
Hemirhamphidae

*Hyporhamphus snyderi* Meek and Hildebrand, M.—Ascends tide streams, Meek and Hildebrand, 1925.

ACANTHOPTERYGII  
Epinephelidae

*Rypticus saponaceus* (Bloch and Schneider), M.—Recorded many miles from the shore in muddy pools and bayous, on or near the Panama Canal. For synonymy see the recent revision of Schultz and Reid, 1939.

Haemulidae

*Pomadasys bayanus* Jordan and Evermann, M(F).—Meek and Hildebrand, 1925.

*Pomadasys macracanthus* (Günther), M?—Meek and Hildebrand, 1925.

Gerridae

*Diapterus axillaris* (Günther), M.—Meek and Hildebrand, 1925.

Carangidae

*Oligoplites saurus* (Bloch and Schneider), M.—Ascends tide streams, Meek and Hildebrand, 1925.

Mugilidae

*Agonostomus monticola* (Bancroft), M(F).—The distribution in Middle America and the West Indies suggests that this freshwater species is euryhalin.

*Agonostomus nasutum* Günther, M(F).—Same as *A. monticola*.

Centropomidae

*Centropomus unionensis* Bocourt, M.—Meek and Hildebrand, 1916; Hildebrand, 1939.

Gobiidae

*Chonophorus banana* (Cuvier and Valenciennes), M(F).—Meek, 1914, says all species of this genus are freshwater. No sea water records have been found. The distribution on both coasts of Middle America and the islands of the West Indies strongly suggests euryhalinity.

Eleotridae

*Eleotris picta* Kner and Steindachner, M(F).—Meek and Hildebrand, 1916; Hildebrand, 1939.

In addition to the foregoing species, some indication was found that the following fishes may possibly belong on the list: *Netuma oscula* (Jordan and Gilbert), *Arius tuya* Meek and Hildebrand, *Aulophallus elongatus* (Günther), *Pomadasys branichi* (Steindachner), *Chonophorus nelsoni* Evermann and *Gillichthys detrusus* Gilbert and Scofield.

**Fishes of the East Coast of North America, North of Southern Florida  
that are Recorded from both Freshwater and Seawater**

CYCLOSTOMI  
Petromyzonidae

*Petromyzon marinus* Linnaeus, A.

ELASMOBRANCHII

BATOIDEI  
Pristidae

\**Pristic pectinatus* Latham, M.—Various authors, see Smith, 1936; Jordan, 1925, says he never took any in the open sea. They are taken in pure sea water by shrimp trawlers in Texas.

Dasyatidae

\**Dasyatis sabina* (Le Sueur), M.—Many authors, see Gunter, 1938b.

## OSTEICHTHYES (TELEOSTOMI)

## CHONDROSTEI

## Acipenseridae

*Acipenser brevirostrum* Le Sueur, A.

*Acipenser oxyrinchus* Mitchill, A.

## ISOSPONDYLI

## Clupeidae

*Alosa sapidissima* (Wilson), A.—Recorded from Nova Scotian banks by Vladikov, 1936.

*Pomolobus aestivalis* Mitchill, A.

*Pomolobus mediocris* (Mitchill), A.

*Pomolobus pseudoharengus* (Wilson), A.—Recorded from Nova Scotian banks by Vladikov, 1936.

*Brevoortia tyrannus* (Latrobe), M.—Young of this species have been observed in fresh-water in the Chesapeake Bay region; personal communications, of V. D. Vladikov and S. F. Hildebrand.

## Megalopidae

\**Tarpon atlanticus* (Cuvier and Valenciennes), M.—Many authors; Hildebrand, 1937.

## Elopidae

\**Elops saurus* Linnaeus, M.—Reported from the St. Johns River at Welaka, Florida, 103 miles above the mouth, where the salinity has been found to range from 167 to 177 parts per million; personal notes of Dr. A. F. Carr, Jr.

## Dorosomidae

*Dorosoma cepedianum* (LeSueur), F.—According to Hildebrand and Schroeder, 1928, this fish is rare in pure salt water.

## Salmonidae

*Salmo salar* Linnaeus, A.

*Salvelinus fontinalis* Mitchill, A.—Bigelow and Welsh, 1925, say the fish never leave the estuary of the home stream; Vladikov and McKenzie, 1935, say it is rare in pure salt water.

*Salvelinus alpinus* of authors, A.—According to Dr. Vladikov, personal communication, there are probably no true *S. alpinus* in North America, and the fish so-called will be found to consist of several endemic species; Vladikov, 1933.

*Salvelinus naresi* Günther, A.—The distribution of this species is given as the coasts and rivers of Arctic America.

*Salvelinus arcticus* Günther, A.—Same as *S. naresi*.

## Engraulidae

\**Anchoviella mitchilli* (Cuvier and Valenciennes), M.—Many authors record this fish as entering rivers. Dr. Carl L. Hubbs has written me that he has a good freshwater record.

## Coregonidae

*Stenodus mackenziei* (Richardson), F.—Personal communication, Prof. John R. Dymond.

*Coregonus clupeaformis* (Mitchill), F.—Dr. A. G. Huntsman has taken this fish in "full salt water," personal communication; Norman (1936) considers that the coregonids are descendants of marine fishes that ascended freshwater to spawn.

## Osmeridae

*Osmerus mordax* Mitchill, A.—According to Jordan and Evermann, 1908, this fish is often landlocked; Bigelow and Welsh, 1925.

## ANGUILLOIDEI

## Anguillidae

\**Anguilla bostoniensis* (Le Sueur), C.

## Ariidae

\**Bagre marina* Mitchell, M.

\**Caleichthys felis* Linnaeus, M.—Regan, 1906-08, says these two ariid catfish enter freshwater and there are many indications in the literature that this is correct. The first indubitable records were notes of Dr. A. F. Carr, Jr., recording the two species from Homosassa Springs, Florida.

## CYPRINODONTES

## Cyprinodontidae

*Fundulus heteroclitus* (Linnaeus), F(M).—This fish ascends barely to the edge of freshwater to spawn.

*Fundulus majalis* (Walbaum), F(M).—Hildebrand and Schroeder, 1928.

*Lucania parva* (Baird and Girard), F(M).

\**Cyprinodon variegatus* Lacépède, F(M).—Many authors, Smith and Bean, 1899.

## Poeciliidae

\**Mollienisia latipinna* Le Sueur, F.

## SYNENTOGNATHI

## Belonidae

\**Strongylura marina* (Walbaum), M.—Smith and Bean, 1899, and many authors.

## ANACANTHINI

## Gadidae

*Microgadus tomcod* (Walbaum), M.—According to Jordan and Evermann, 1908, this fish has been taken sixty miles above the mouth of the Kennebec River.

## ACANTHOPTERYGII

## Gasterosteidae

*Apeltes quadracus* Mitchell, M.—This is primarily a salt and brackish water fish, which sometimes enters freshwater. Bigelow and Welsh, 1925, say that they have no records from the open sea.

*Gasterosteus aculeatus* Linnaeus, M(F).

## Syngnathidae

*Syngnathus fuscus* Storer, M.—Hildebrand and Schroeder, 1928.

*Syngnathus scovelli* (Evermann and Kendall), M.—Dr. Hubbs has written me that this species occurs across practically the whole peninsula of Florida.

## Atherinidae

\**Menidia beryllina* (Cope), M(F).—Hildebrand and Schroeder, 1928.

*Menidia menidia* (Linnaeus), M.—According to Hildebrand and Schroeder, 1928, this fish enters freshwater, though rarely.

## Mugilidae

\**Mugil cephalus* Linnaeus, M.—See West Coast list.

\**Mugil curema* Cuvier and Valenciennes, M.—See West Coast list.

## Carangidae

\**Caranx latus* Agassiz, M.—Meek, 1914.

\**Caranx hippos* (Linnaeus), M.—See West Coast list.

## Lutianidae

\**Lutianus griseus* (Linnaeus), M.—This snapper ascends streams of the Atlantic Coast of the United States, Hildebrand and Schroeder, 1928, as it does in Mexico and southward, Hubbs, 1936. It has been recorded from Homosassa Springs and canals and creeks near Naples, Florida, notes of Dr. A. F. Carr, Jr.

\**Lutianus apodus* (Walbaum), M.—Recorded from Homosassa Springs, Florida, personal notes, Dr. A. F. Carr, Jr.



## Sparidae

- Lagodon rhomboides* (Linnaeus), M.—Recorded from Homossasa Springs and Six-mile Creek, near Tampa, Florida, notes of Dr. Carr.  
*Archosargus probatocephalus* (Walbaum), M.—According to Dr. Carr, this fish is widely distributed in freshwater of the southern portion of the peninsula of Florida.

## Gerridae

- \**Eucinostomus californiensis* (Gill), M.—Several authors, see West Coast list.

## Moronidae

- Morone americana* (Gmelin), A.  
*Roccus saxatilis* (Walbaum), A.

## Sciaenidae

- \**Leiostomus xanthurus* (Latrobe), M.—Hildebrand and Schroeder, 1928; Hildebrand and Cable, 1930.  
\**Micropogon undulatus* (Linnaeus), M.—This croaker was reported from Lake Yzabel by Vaillant and Bocourt, Miss. Sci. Mex. Poiss. 1874. Dr. Hubbs has written me that he took this fish in Bayou Minette in Florida in freshwater.  
*Pogonias cromis* (Linnaeus), M.—Reported from the lower Mystic River, Boston, by Bigelow and Welsh, 1925; also reported from Lake George and the St. Johns River at Welaka, Florida, personal notes of Dr. A. F. Carr, Jr.  
\**Sciaenops ocellatus* (Linnaeus), M.—Recorded from Lakes Harney and George and Homossasa Springs, Florida, notes of Dr. Carr.

## Otolithidae

- \**Cynoscion nebulosus* (Cuvier and Valenciennes), M.—Recorded from Homossasa Springs, Florida by Dr. Carr.

## Eleotridae

- \**Evorthodes lyricus* (Gill), M.—Meek and Hildebrand, 1928, as *E. breviceps*; for corrected synonymy see Ginsburg, 1931.

## Gobiidae

- \**Dormitorator maculatus* (Bloch), M(F).—Recorded by many authors from brackish waters and rivers. According to Meek, 1914, fish of this genus return to the sea. Evermann and Marsh, 1900, say it is taken on snapper banks.  
*Gobiosoma boscii* (Lacépède), M.—Hildebrand and Schroeder, 1928, took this goby in fresh, brackish and salt water.

## Echeneididae

- \**Echeneis naucrates* Linnaeus, M.—Recorded from Homossasa Springs, Florida by Dr. A. F. Carr, Jr.

## Bothidae

- \**Citharichthys spilopterus* Günther, M.—Meek, 1914.

## Paralichthidae

- Paralichthys dentatus* Linnaeus, M.—Bigelow and Welsh, 1925, and other authors state that this flounder goes up rivers beyond the influence of salt water.  
\**Paralichthys lethostigmus* Jordan and Gilbert, M.—Recorded from Lake George and St. Johns River, Florida by Dr. A. F. Carr, Jr.

## Achiridae

- \**Trinectes maculatus* (Bloch and Schneider), M.—Jordan and Evermann, 1900, and various authors, see Gunter, 1938b.

## Probably Euryhalin Fishes

## ELASMOBRANCHII

## EUSELACHII

## Carchariidae

- Carcharias milberti* Valenciennes, M.—This shark enters the Cooper and several other rivers around Charleston, South Carolina, but it is not known to get entirely beyond the influence of the sea, personal communication, Mr. T. K. Ellis.

*Scoliodon terra-novae* (Richardson), M.—This shark enters the Pascagoula River, possibly not above brackish water, personal communication, Mr. Stewart Springer.

*Mustelis canis* (Mitchill), M.—This shark enters tidal freshwater in the North East River, Maryland, personal communication, Dr. Henry W. Fowler.

#### Sphyrnidae

\**Sphyrna zygaena* (Linnaeus), M.—This shark has been reported from tidal freshwater, North East River, Maryland, personal communication, Dr. Fowler.

#### OSTEICHTHYES (TELEOSTOMI)

##### ISOSPONDYLI

##### Coregonidae

*Leucichthys artedi* (Le Sueur), F.

*Prosopium quadrilaterale* (Richardson), F.—The two above species range far into bay waters, many Canadian authors.

##### Cyprinodontidae

*Fundulus luciae* (Baird), F(M).—Breder, 1929.

##### Poeciliidae

*Gambusia affinis* (Baird and Girard), F.—Dr. Hildebrand, personal communication, states that *G. holbrooki*, which workers with the poecilids consider to be a subspecies of *G. affinis*, is sometimes taken in strongly salt water in North Carolina.

##### ANACANTHINI

##### Gadidae

*Gadus morrhua* Linnaeus, M.—This fish has been reported in freshwater ponds connected to the sea, in Canada, but never corroborated by an ichthyologist; personal communication, Dr. A. G. Huntsman. It has been reported from freshwater in Denmark by Feddersen, 1879.

##### ACANTHOPTERYGII

##### Gasterosteidae

*Pungitius pungitius* Linnaeus, M.—This is a salt and brackish water fish, but Bigelow and Welsh, 1925, say it is never taken in sea water.

##### Carangidae

\**Oligoplites saurus* (Bloch and Schneider), M.—See West Coast list.

##### Otolithidae

*Cynoscion regalis* (Bloch and Schneider), M.—This fish is taken in river mouths, Bigelow and Welsh, 1925.

##### Rachycentridae

\**Rachycentron canadus* (Linnaeus), M.—Fisher, 1891, records this fish from the mouth of the Croton River, at Sing Sing, New York, near where it enters the Hudson. Dr. John R. Greeley has written me that brackish water ascends to this locality.

#### Fishes of the East Coast of Mexico and Middle America, North of the Southern Boundary of Panama, Recorded from both Freshwater and Sea Water

##### ELASMOBRANCHII

##### EUSELACHII

##### Carcharidae

*Carcharias platyodon* (Poey), M.—Gunter, 1938b.

##### OSTEICHTHYES (TELEOSTOMI)

##### HOLOSTEI

##### Lepisosteidae

*Lepisosteus tristoechus* Lacépède, F.—I assume this is the correct name for the fish

often referred to as *Atractosteus* or *Lepisosteus spatula*. It is generally reported in brackish water. The writer once took one in an otter trawl in the open sea, three-fourths of a mile off shore from Quartre Bayou Pass, Louisiana.

## ISOSPONDYLI

## Dorosomidae

*Signalosa atchafalaya* Evermann and Kendall, M.—This fish was described from fresh-water. It is estuarine and marine and is sometimes taken in trawl hauls in the open sea, see Gunter, 1938a.

## Engraulidae

*Anchovia macrolepidota* (Kner and Steindachner), M.—Many authors.

*Anchovia parva* (Meek and Hildebrand), M.—This fish has possibly crossed the Isthmus of Panama through the canal, see Hildebrand, 1939.

*Anchovia spinifera* (Cuvier and Valenciennes), M.—See West Coast list.

## CYPRINODONTES

## Cyprinodontidae

*Fundulus grandis* Baird and Girard, F(M).

## Poeciliidae

*Mollienisia spheonops* (Cuvier and Valenciennes), F.—Jordan and Evermann, 1900; 1908, and other authors.

## SYNENTOGNATHI

## Belonidae

*Strongylura scrutator* (Baird and Girard), M.—Hubbs, 1936.

*Strongylura timucu* (Walbaum), M.—Many authors.

## ACANTHOPTERYGII

## Centropomidae

*Centropomus pectinatus* Poey, M.—See West Coast list.

*Centropomus parallelus* (Poey), M.—Jordan and Evermann, 1908; Meek and Hildebrand, 1925; Hildebrand, 1939.

*Centropomus undecimalis* (Bloch), M.—Jordan and Evermann, 1908; Meek, 1914.

## Haemulidae

*Pomadourys crocro* (Cuvier and Valenciennes), M.—Meek and Hildebrand, 1925.

## Gerridae

*Gerres cinereus* (Walbaum), M.—See West Coast list.

## Eleotridae

*Gobiomorus dormitor* Lacépède, M(F).—According to Jordan and Evermann, 1900, and Meek, 1914, this species returns to the sea.

*Guavina guavina* (Cuvier and Valenciennes), M(F).—According to Meek, 1914, fishes of this genus return to the sea; Meek and Hildebrand, 1928.

## Probably Euryhalin Fishes

## OSTEICHTHYES (TELEOSTOMI)

## SYNENTOGNATHI

## Belonidae

*Strongylura notata* (Poey), M.—Hubbs, 1936.

## ACANTHOPTERYGII

## Syngnathidae

*Oostethus lineatus* (Valenciennes), M(F).—According to Hildebrand, 1939, this pipe-fish breeds in freshwater. Meek and Hildebrand in their collections in Middle America took it in brackish water.

## Atherinidae

*Thyrina chagresi* Meek and Hildebrand, F.—Recorded from brackish water, Meek and Hildebrand, 1923.

## Mugilidae

*Agonostomus monticola* (Bancroft), M(F).—See West Coast list.

*Agonostomus nasutum* Günther, M(F).—See West Coast list.

## Gerridae

*Gerres plumieri* Cuvier and Valenciennes, M.—Regan, 1906-8.

*Diapterus rhombeus* (Cuvier), M. Goes far up brackish streams, Meek and Hildebrand, 1925.

## Sciaenidae

*Micropogon furnieri* (Desmarest), M.—Hubbs, 1936.

## Gobiidae

*Chonophorus banana* (Cuvier and Valenciennes), M(F).—See West Coast list.

*Gobionellus claytonii* (Meek), M.—Meek, 1904, 1914; see locality records, Ginsburg 1932.

*Coboides broussonettii* Lacépède, M.—This goby is distributed from the West Indies to Brazil and is recorded many times from rivers.

In the course of investigating the records indications were found, but none definite, that the following species possibly belong to the list: *Synbranchus marmoratus* Bloch, *Fundulus similis* (Baird and Girard), *Harengula pensacolatae* Goode and Bean, *Menidia lisa* Meek, *Mugil trichodon* Poey, *Lobotes surinamensis* (Bloch), *Pomadasys starri* Meek and *Chonophorus mexicana* (Günther).

Several marine fishes of wide distribution have been reported from freshwater in other parts of the world. No record of their invasion of freshwater in North and Middle America has been found. Boulenger took the barracuda, *Sphyræna guachancho* Cuvier and Valenciennes, in the Congo River (Les Poissons du Bassin du Congo, p. 364, 1901). Feddersen (1879) reported the dogfish shark, *Squalus acanthias* Linnaeus, from freshwater in Denmark. According to Smith (1936), the rays, *Stoasodon narinari* (Euphrasen) and *Pteroplatea micrura* (Schneider), have been reported from freshwater in Siam and Borneo. The swordfish, *Xiphias gladius* Linnaeus, has been known to go up the rivers Parrett, Vannes and Weser in Europe, (Goode, 1883).

## Discussion

The number of elasmobranchs on the list is noteworthy. So many elasmobranchs invade freshwater that the German students have referred to them as a group, the "Süßwasser elasmobranchier." This fact, although attested to by the literature for years, is not well-recognized by American zoologists. Smith (1936) called attention to the fact that it is commonly stated that elasmobranchs do not enter freshwater and gave records of fifty-two species in the freshwaters of the world. On July 2, 1940, the newspapers of the lower Rio Grande Valley gave an account of a five hundred-pound shark that was caught in a cotton field near Raymondville, Texas, about one hundred miles from the river mouth, where it came in through an irrigation canal.

Schlieper (1935) has called attention to the fact that the fishes of one genus may be quite variable with respect to their euryhalin proclivities. Nevertheless, euryhalinity runs in families. Members of the Acipenseridae, Salmonidae, Clupeidae, Cyprinodontidae, Gasterosteidae, Centropomidae, Gerridae,

and Gobiidae, as well as many Elasmobranchii and Heterosomata are prone to have this characteristic. Euryhalin species on one side of the continent often have their counterpart on the other side, if the family is represented on both shores.

The ability of aquatic animals to undergo salinity changes is closely dependent upon their excretory powers and organs. This question has received considerable attention in the reviews of Schlieper (*op. cit.*) and Smith (1932). Marshall and Smith (1930) stated that with the assumption of the marine habitat by teleost fishes the glomerular development becomes poor. Schlieper, and other workers cited by him, have shown that freshwater invertebrates have excretory organs much better developed than marine invertebrates. He makes the statement that many stenohalin, marine, teleost fishes even have aglomerular kidneys. The list shows, however, that the aglomerular pipefishes have a tendency to invade freshwater. Possibly the pipefishes have developed "ersatz" mechanisms to take care of their excretory problems in that medium.

It is generally accepted by biologists as a fact that marine animals in the tropics invade rivers much more than in the temperate zones. There are some reasons why this seems plausible, but in all rivers with wide estuaries there is probably invasion by marine animals. There seems to be no overwhelming predominance of tropical fishes on the list and possibly the contrast between the tropics and northern climes, in this respect, is not so great as it is generally considered to be.

Table I is compiled from the list and gives the actual number of euryhalin species and the percentage for the groups shown in the tables. The numbers used in calculating the percentages were taken from the check list of Jordan, Evermann, and Clark (1930). Use of this list may inject a certain amount of error, for its geographical range is somewhat greater than that of the list compiled here, but it is the best information available. In these and the following calculations species in the Probably Euryhalin group were used, for their inclusion did not materially change the results. It is clear that while large numbers of higher fishes are euryhalin, the percentage is much greater for the primitive fishes. The lower 11.9 per cent of the fishes of North and Middle America, cyclostomes to Isospondyli, contain 35.6 per cent of the euryhalin and nearly euryhalin species, as determined by this list. Whether this situation holds for the rest of the world or the whole Northern Hemisphere is not known, but there is reason to believe that the percentage is greater for the specialized fishes in the tropics. It is believed that the results in Table 1 represent a true situation with respect to North America. Many facts bearing on it are doubtless still shrouded in mystery and the meaning is far from being understood. Future work in the zoogeography, phylogeny and physiology of fishes will possibly clarify to some extent the reasons for this state of affairs among the euryhalin fishes of North America.

It is considered true in general that as animals progress from lower to higher in the evolutionary scale that they become increasingly independent of

TABLE 1.—The figures from this table were derived from the list of euryhalin species given in this paper. In the first two lines the number of species in the groups listed at the head of the table are shown. The fourth line gives the number of species in the same groups in the check list of fishes of North and Middle America by Jordan, Evermann and Clark. These figures are used in calculating the percentages shown in the last line. Many of the acanthopterygian fishes are euryhalin but the percentage euryhalin is greater for the more primitive fishes.

	Cyclotomes	Elasmobranchs	Ganoids	Isopondyli	Isopondyli to Acanthopterygii	Acanthopterygii
Number on the list	4	5	5	38	16	64
Number in the Probably Euryhalin Class	(0)	(4)	(0)	(5)	(10)	22
Total	4	9	5	43	26	86
Number of species in the check list of Jordan, Evermann and Clark	14	158	18	301	1,191	2,448
Percentage of each group that is euryhalin or near euryhalin	28.6	5.7	27.8	12.6	2.2	3.5

the environment. This independence may, in one sense of the word, be said to depend on isolation. Bayliss (1924) said "... as we ascend the scale of evolution, we find that the blood is maintained at nearly constant osmotic pressure by regulative mechanisms." Then it is to be expected that the higher fishes would become more and more independent of the external environment and as the evolutionary scale was traversed more and more of them would become able to go from sea water to freshwater and the reverse, without difficulty. The percentage of euryhalin fishes shown by Table 1, however, is much less for the higher fishes. Either the theory is not true for the fishes as a group or the specialized fishes have greater regulatory power over the internal environment only within narrow limits of the external environment and cannot survive when these limits are passed. If the more primitive fishes have less regulatory power over their blood systems as the environment undergoes wide changes, then they must simply be able to tolerate wider changes than the specialized fishes can. In that case, euryhalinity may be a problem of cellular physiology as well as one of the vascular and excretory systems.

There is a relationship between the kind of fishes that are euryhalin and the latitude. Table 2 gives a comparison of the number of euryhalin species in the Acanthopterygii and below the Acanthopterygii for the four divisions of the list. Table 3 shows the same thing for the east and west coasts combined. It is seen that in the northern waters the euryhalin fishes are predominantly of a lower order, while in the tropics they are of a higher order. This condition would be more striking if the four divisions of the list were made at the mean annual isotherm of 20.0° C. in the sea. Obviously, many tropical species are included by extending the northern part of the Atlantic Coast list to southern

TABLE 2.—This table gives the number of species of fishes below the Acanthopterygii and in the Acanthopterygii for four divisions of the list.

	West Coast of North America, north of Mexico	West Coast of Mexico and Mid- dle America	East Coast of North America, north of southern Florida	East Coast of Mexico and Mid- dle America
Below the Acanthopterygii	23	12	41	26
Acanthopterygii	11	36	34	40

TABLE 3.—Here the figures for east and west coasts, shown in Table 2 are combined. If the same species is present on both coasts, it is counted only once. These tables indicate that in temperate North America euryhalin fishes less specialized than the Acanthopterygii predominate, while in the subtropics and tropics euryhalin fishes are predominantly acanthopterygian.

	North America, north of Mexico and southern Florida	Mexico and Middle America
Below the Acanthopterygii	36	65
Acanthopterygii	66	44



TABLE 4.—This gives the number of species from the whole list placed in the various environmental categories, explained in the text. In North America, marine fishes that enter freshwater outnumber freshwater fishes that enter the sea by almost nine to one.

Environmental affinity of species	Freshwater	Marine	Freshwater (Marine)	Marine (Freshwater)	Anadromous	Catadromous
Number	12	106	8	17	31	1

Florida. If the anadromous fishes were excluded from the list, the distinction would not be so apparent, for the anadromous fishes are most prominent in the northern part of the continent and, with the exception of the two members of the Moronidae, all are below the spiny-rayed fishes. The distribution of the anadromous fishes by groups is: cyclostomes 4, ganoids 5, Isospondyli 20, and Acanthopterygii 2. There is no anadromous fish recorded from Mexico and Middle America. The reason for this latitudinal variation becomes largely a question of why the anadromous fishes are of a lower order and why they are confined to northern climes.

Meek (1904, 1908), Hubbs (1936), Myers (1938) and others have pointed out the affinities of Mexican and Middle American fishes with the tropics rather than with North America. Possibly, the predominance of the higher fishes in the euryhalin category is typical of the tropics as a whole. No reference to this matter has been found in the literature, but it was noticed in a general way by at least one ichthyologist. The late Dr. C. H. Gilbert once told Dr. Carl L. Hubbs, several years ago, that he had observed that greater numbers of higher marine fishes invaded rivers in the tropics than they did in northern zones.

Table 4 shows that the purely marine fishes on the list outnumber the freshwater species by nine to one. This figure was arrived at after the anadromous, catadromous, and species marked M(F) and F(M) were excluded. According to Macfarlane (1923) there are about 13,000 species of marine fishes and 8,000 species of freshwater fishes in the world. Assuming that roughly the same ratio applies to North America, then we can say that marine species outnumber freshwater species about two to one. This is not enough to account for the predominance of marine species in the North American euryhalin category. If, as modern theory has it, fishes arose in freshwater and secondarily invaded the sea, then their descendants seem to be trying to reinvade freshwater. However, I am inclined to the opposite view, namely, that the marine fishes of to day are activated by the same stimuli that affected their prototypes, the marine ancestors of land animals, long ago.

A priori consideration might lead to the conclusion that marine animals, on account of loss of salts in more dilute media, would be more rigidly stenohalin than freshwater animals. This seems not to be the case. Bay and estuarine fauna is predominantly marine. Annandale (The marine element in the fauna of the

Ganges, Bijdr. Dierk., Amsterdam, 1922) working on the Ganges Delta, and Pearse (1936), who quoted him, are the only writers I know that mention this significant fact. Apparently, marine animals can tolerate lowered salinity better than freshwater fauna can tolerate a raised salinity and, as a whole, they may be said to be more euryhalin. The predominance of marine species among the euryhalin fishes of North America seems to be another aspect of this general situation. Not only is bay and estuarine fauna chiefly marine, but marine animals enter freshwater more often than freshwater animals invade the sea. The marine fishes of North America that invade freshwater are a relatively small percentage of the total, and yet their numbers are much greater than those of freshwater fishes in the sea. The question arising: Why do so few freshwater fishes invade the sea?

### Summary

For purposes of this paper a euryhalin fish is defined as one that is found in both freshwater and sea water under natural conditions. A list is compiled of all fishes, including cyclostomes and elasmobranchs, that have been recorded from both habitats in North and Middle America, north of the southern boundary of Panama. The list is divided into four parts: Pacific Coast south to Mexico, west coast of Mexico southward, Atlantic Coast to the southern part of the east Florida Coast, and the east coast of Mexico southward. The Gulf Coast of the United States is left out because all but three species of fishes from that region are included on other divisions of the list. A capital letter is placed by each species classifying the fishes as catadromous, anadromous, freshwater or marine. Fishes of marine families living in freshwater are labeled M(F) and conversely species with freshwater affinities living in salt water are labeled F(M). In some instances this classification may be arbitrary. For some fishes there were strong indications that they belonged on the list but no definite records could be found. These species were listed under the heading Probably Euryhalin and they were included in making up the tables given, for their exclusion did not materially change the results.

There are 173 species on the list, including forty-one probably euryhalin species. The percentage of euryhalin species is much greater for the primitive fishes. The lower 11.6 per cent of the fishes of North America contain almost 36.0 per cent of the euryhalin species. There are no anadromous fishes south of the northern boundary of Mexico. North of Mexico the majority of euryhalin fishes are of the lower order while south of Mexico they are of a higher order, (Tables 2 and 3). This is chiefly due to the fact that anadromous fishes are of a lower order (Isospondyli) and of northern distribution. Marine fishes are recorded in freshwater nine times oftener than freshwater species are found in the sea, which is much greater than the two to one approximate proportions of the two groups. This is thought to be related to and in some respects an extreme of the general situation that estuarine and brackish water fauna is chiefly marine. Marine fishes tend to be euryhalin more than freshwater fishes do.

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## Anomalous Seasonal Coat-Color-Changes in a Small Male Bonaparte's Weasel

(*Mustela cicognanii cicognanii* Bonaparte)\*

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### Introduction

During two years of an experimental study of control of seasonal changes of color and pelts in weasels, one male Bonaparte's weasel (*Mustela cicognanii cicognanii* Bonaparte) among the controls on normal light-cycles and relatively moderate changes of temperature, was much smaller than two female Bonaparte's weasels also used in the experiment. He possessed a much shorter tail with shorter hair and small black, but not bushy, tip. The time of his autumn-winter molt and the amount of change to white did not correspond with those of the other Bonaparte's weasels nor with those of New York weasels (*Mustela frenata noveboracensis*) under similar conditions, but were intermediate. His changes of color during the two winter and spring seasons in which he was under observation were not alike, although the temperature of his environment varied in much the same degree each year. They are therefore described and discussed in relation to the observed changes in his habits relating to daily exposures to light, which seem partly to condition them.

### Case History

He was received in a consignment of living weasels from a trapper in Pennsylvania on May 30, 1939. He was judged to be a young animal, probably a female Bonaparte weasel, because he was much smaller than two females of that species, and handling for sexing was avoided for fear of accident and loss of animals. His sex became evident when he came into full sexual potency in the following spring and his testes hung low in the scrotum, although he has remained smaller than the others of that species through more than two years. Dr. Glover M. Allen has identified him as an abnormal *Mustela cicognanii cicognanii* Bonaparte. He was confined in a den-runway-system described by Bissonnette and Bailey (1940), with other weasels as one of the controls on normal light-cycles, in a basement room from May 30, 1939, until April 12, 1941, except as stated below. He was then changed over to experimental light-cycles. Observations covered almost two and one-half years and two cycles of change of pelt. He remained throughout in apparent good health on a food-ration of whole raw milk, water, and lean meat each day, with liver once or twice a week and a living mouse or a starling's entrails with some flesh once a

\* Aided by a grant from the Penrose Fund of the American Philosophical Society, 1939.

week, for vitamins. Some cod-liver-oil concentrate and a pinch of brewer's yeast were added to the milk part of the time.

The temperature in the room was cool in summer (64-70° F.) and warmer than outside in winter (50-72° F.), when it was heated only by influx of warm air from the basement halls, heated to about 70-74° F., to replace air drawn off by an electric fan in one window. No attempt at rigorous control of temperature was made; but the temperature throughout the year was much more uniform and less variable than that outside or in the woods and fence-rows where these animals normally live. Since this did not affect the molts and changes of color in the other weasels used in the experiment it is not believed that it was a factor in causing the anomalous pelt-changes of this animal, especially because his first assumption of white hairs occurred after and while he was being placed with the other controls each night in a warmer room, to be out of experimental lighting, and ceased too long after such transfer was discontinued. The opposite changes of pelt should have resulted if temperature change were a factor in inducing such changes. The transfer was begun in December, 1939, and stopped in February, 1940.

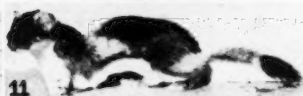
#### Observations

His coat underwent no observable change throughout the summer and autumn, through December (Fig. 1, November 27, 1939), when another Bonaparte weasel turned white or "gray-back" and New York weasels took on a lighter brown as usual in this locality (Goodwin, 1935; Bissonnette and Bailey, unpublished data). During January his coat began to turn white up the legs and sides of the body, along the under side of the tail, and around the ears and cheeks, with lips, nose and forehead remaining brown (Fig. 2, January 26, 1940). Whitening proceeded up the sides, over the shoulders, and along the tail from base toward tip (Fig. 3, February 6, 1940), with loins and hips becoming gray (Fig. 4, February 23), until it stopped before March 1, when he was still partly brown. Molt and regrowth of hairs had stopped.

#### EXPLANATION OF PLATE

Fig. 1. Coat color of male Least Weasel during summer and until December 25, 1939. Still in "summer" brown. Fig. 2. January 26, 1940. The same weasel. White is spreading upward from feet and belly over limbs and flanks, around ears and on cheeks, and along tail from black tip toward base. Fig. 3. February 6, 1940. White has spread upward over shoulders, hips, and behind ears. Fig. 4. February 23, 1940. Most advanced stage of whitening, with white saddle over shoulders and gray sides and hips. Fig. 5. March 12, 1940. First brown short hairs among the white appear as shadows along the flanks and shoulders. Fig. 6. March 25, 1940. Brown band along shoulders and flank and over hips. Tail becoming brown from tip forward toward base, and anterior surfaces of limbs from above downward. Fig. 7. April 10, 1940. Condition little if any changed since March 25. Fig. 8. June 6, 1940. Change toward brown "summer" coat has stopped. Base of tail still white and parts of hips also. Fig. 9. August 14, 1940. No change. Fig. 10. November 4, 1940. No change. Fig. 11. December 19, 1940. No change. Fig. 12. February 11, 1941. Animal has returned to "summer" brown coat except for white ring next the black tip of the tail. Fig. 13. June 6-Sept. 27, 1941. Little if any change in color. White ring on tail still present. Brown may be slightly darker than in February. Apparent light spots on hips are from light shining on his fur and reflected.





He remained in this condition for a few days only (March 1-10), before short brown hairs began to show through the white along the flanks, the lateral sides of the limbs and the dorsum of the tail (Fig. 5, March 12). The white hairs over these regions were shed and brown appeared on the surface (Fig. 6, March 25). Then white hairs stopped falling out, all hairs became tight in their follicles and browning stopped, leaving the animal white over the shoulders, along the sides of the back and hips, and at the base of the tail (Figs. 7, 8, April 10 and June 6, resp.). He remained in this piebald coat throughout the summer, autumn, and through December (Figs. 9, 10, 11, August 14, November 4, December 19, resp.).

Sometime in January, 1941, he began to shed both white and brown hairs and to take on a new coat. But, instead of assuming "winter white," as he had done about the same time in the preceding winter, he returned to "summer brown" except for a white ring next the black tip and a white stripe along the underside of his tail, before January 11, 1941 (Fig. 12). This time the brown color spread downward and laterally from the ridge of his back and top of his head and from base to tip and dorsum to venter of his tail. This is the usual manner of resumption of brown summer coat in both species of weasel observed with this animal, and secured from the same place in Pennsylvania.

No further change in coat was noted through spring and summer or autumn of 1941, except perhaps some darkening of the color toward summer (Fig. 13, June 6 to September 27). No change was noticeable on December 1, or through February, 1942, whereas another apparently normal Bonaparte's weasel under identical conditions became completely white on or before November 6.

### Discussion

In the absence of more experimental data from controlled studies involving more animals with this one, and from the same locality, we are thrown back largely upon speculation to account for the anomalous molts and color-changes of this animal while under observation. If reduced temperature were the stimulus for change to white, as is generally supposed, this animal, moved into warmer quarters each night, should have become brown instead of partly white in January, 1939. A female Bonaparte's weasel under similar conditions became almost completely white (grey-back). So it is concluded that it was not the change of temperature that modified his pelt cycle, but some other factor in his environment.

It was noticed that some time in November, 1939, he began to spend less time by day in the lighted runway of his pen than previously, only coming out of the dark den very infrequently. This involved a voluntary reduction of his daily light-hours from that time onward and probably for some time before his change of habit was noticed. In January he began to spend more daylight time in the runway again. If change of light-time is the stimulus for molting in this animal, as it appears to be for Bonaparte's and New York weasels in general (unpublished data), these changes in habit could lead to the coat color changes

observed in this animal during winter and spring, 1939-40. If reversal of changes from longer to shorter hours of daily light, before the complete assumption of white coat, can stop a molt short of completion and induce a second in the opposite direction for color, again stopped short of completion by another change in light-time, the anomalous changes in coat-color of this animal can be accounted for. Such changes will account for the incompleteness of both winter whitening and spring browning observed. The differences in amount of whitening over the body indicate that there is variability in the degree or rate of response of various body regions to the internal or endocrine factor or factors mediating the color change. Some parts require higher effective concentrations of these internal factors in the blood or are slower to respond to a given concentration than others. This is shown in the reversal change also. That these internal factors are hormones from the pituitary, and probably the thyroid as well, has been suggested by Bissonnette (1935) for ferrets, and Wright (1941) for weasels.

It is fairly well established that the anterior lobe of the hypophysis can be stimulated by added daily lighting acting through the eyes (Bissonnette, 1938; Legros-Clark, McKeown and Zuckerman, 1939) at least for ferrets. The thyroid is controlled in part at least by the thyrotropic hormone of the pituitary. So both may be involved in the control of pigmentation in developing hair of these animals.

On the basis of the above reasoning any unusual behavior of a weasel, capable of blanching in winter, in relation to its exposure to light, will be expected to bring about either normal or anomalous molt-cycles and changes of color in members of this species, in nature as in captivity, if these changes in habit involve sufficient degree of change in daily light-time. Difference in threshold of responsiveness of various parts of the body, or different speeds of response, will account for patterns of coat color and for incomplete molts and changes of color in either direction. This will account for "gray-backs" as well as for piebald animals.

For experimental purposes the locality of origin of all animals used in any one experiment, using comparison of color-cycles, must be the same to be strictly comparable; and, in addition, previous molting history of an individual must also be known if possible. Again, patterns of molt differ in different seasons for the same animal if the environmental conditions are not the same or if the habits of the animal change in regard to the external modifying factor or factors. Selection in relation to their immediate environment and its changes from summer to winter conditions, or lack of change effective for the animals, make either white or brown color in winter protective, by rendering them inconspicuous against a white or a dun-colored background, or act as lethal in making them conspicuous, as the case may be. They become easily caught by enemies and find it difficult or impossible to catch their own prey, if they are carnivores like weasels. If colored differently from their surroundings they are killed in large numbers and at the same time tend to starve, leaving few to survive and breed, and those for the most part having the best camouflage relation to the environment. This gives selection within an originally variable species, in locali-

ties usually snowy in winter, in favor of members turning white, increasing their numbers relatively; and against those that remain brown in the snowy months, decreasing their relative numbers. The reverse obtains in localities not snowy in winter. Not all members of the same species, however, always conform or behave in the same manner, but the mean of variation shifts in one direction or the other. Complete conformity is never reached in nature although variability may be reduced in this way, until the members of a species usually do or do not turn white in winter. Exceptions, such as the animal described above, continue to occur and are interesting as illustrating the persistence of variability even in a highly selected local race.

The stimulus for change of pelt-color must precede that change by sufficient time to allow for a latent or preparatory period before color-change in the hair begins, and the stimulus must be operative during this time to induce molt and control regrowth and altered pigmentation of the new coat. The same stimulus or degree of environmental change can come to have different effects upon local populations of the same species depending upon their previous selections in terms of winter coat-color. Such changes in the reactions of members of the same species may resemble the differences met with in nearly related species like the different weasels found in neighboring localities. Then, too, sex differences in behavior relating to daily period of exposure to light may lead members of one sex to spend more time, or less, in the dens than the other. In this way one sex may tend to become white regularly while the other does not, or to assume intermediate color-patterns more often than the other sex. Reaction to such changes also may lead to one animal's becoming white or partly white in one winter season and its remaining brown in another winter. Occasionally an animal may even fail to assume the normal amount of brown in summer although that season may be much the same as others in climatic or daylight conditions, as this animal appears to have done. Although he is still smaller than other Bonaparte's weasels of either sex, he is at least two and one-half years old and his failure to become normally white in winter cannot be attributed to immaturity. His change of habits in relation to his environment, rather than, or in addition to, changes in that environment, appear to have conditioned his changes in pelt and color. He may be said to have controlled his environment to this extent and thereby controlled his coat-color cycle as above described.

### Summary

The molts and changes of coat-color undergone by a very small male Bonaparte's weasel (*Mustela cicognanii cicognanii* Bonaparte) during two and one-half years in captivity are described and shown in a series of photographs. By molting and replacing hairs, he became partly white in January and February, 1940; partly returned to brown in March, 1940; remained piebald throughout summer and autumn; and became almost wholly brown again on his upper parts in January and February, 1941. He remained in this, the usual summer condition except for a small white ring near the tip and a white stripe along the underside of his tail, until December, 1941.

Until April, 1941, he was on normal light cycles. Experimental control of lighting was begun in April and continued through December, 1941, and January and February, 1942. The anomalous changes in coat-color of this animal followed changes in habits in regard to time spent in the light and in the dark den. These changes of color do not appear to have been due to changes of environmental temperature, which was such as to be expected to induce changes of color in the opposite direction to those that did occur, if change of temperature were the effective stimulus. It is suggested that change in relative period of exposure to light is more probably the conditioning factor.

The significance of such changes in relation to the general problem of natural and experimental environmental control of molting and color-changes in weasels is discussed. It is pointed out that altered relations to available light could explain or account for the reactions of this animal if daily duration of exposure to light is the variable factor which conditions molts and color-changes in weasels of this species, and in this animal in particular.

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## A Generic Revision of the Crayfishes of the Subfamily Cambarinae (Decapoda, Astacidae) with the Description of a New Genus and Species\*

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Recent students of the crayfishes are finding the conservative treatment given by Ortmann and Faxon to the species comprising the genus *Cambarus* less and less satisfactory in the light of increasing knowledge of the group. Ortmann and Faxon divided this genus into a number of subgenera, sections and groups, some of which, because of their distinctiveness, seem to deserve the status of higher categories. As long as *Cambarus* was small and the available information scanty, the conservative classification was not only logical but definitely practical. Now, with more accurate knowledge of specific ranges, and with the finding of many new species, new relationships have been discovered which are not adequately expressed by Ortmann's and Faxon's treatments. The splitting of the old genus *Cambarus* into two genera by Creaser (1933) has done little to relieve the congestion.

In this paper, I am proposing that the genus *Cambarus* (as now defined—i.e., exclusive of the species belonging to *Faxonius*) be divided into four genera, *Procambarus*, *Paracambarus*, *Cambarellus*, and *Cambarus*; furthermore, it is here shown that the name *Faxonius* must be supplanted by *Orconectes* on grounds of priority. In addition I am proposing a new monotypic genus, *Troglocambarus*, for a rather remarkable cavernicolous species which inhabits the solution cavities in the north-central part of the Florida peninsula. Under each of these six genera I have listed the species which have been described since Faxon prepared his check list in 1914.

### Historical Outline of the two Genera *Cambarus* and *Faxonius*

The first American crayfish was described by Fabricius in 1798, and called *Astacus bartonii*. The description is very short, and the locality from which his specimens were taken is not given.

In 1817 Rafinesque described four species from North America, *Astacus limosus*, *fossor*, *ciliaris*, and *pusillus*. Of these only *limosus* (of which *affinis* Say is a synonym) is of interest here.

In 1835 *Astacus blandingii* was described by Harlan, the locality being given as South Carolina.

In 1884 Th. Tellkampf in J. Mueller, described *Astacus pellucidus* from Mammoth Cave, Kentucky.

\* Contribution from the Department of Biology, University of Florida.

The name *Cambarus* was introduced by Erichson in 1846. In this "Unter-gattung" he included *pellucidus*, *affinis* [=synonym of *limosus*], *carolinus*, *bartonii*, *blandingii*, *wiegmanni*, *mexicanus*, *cubensis*, and *chilensis*.

Girard in 1852 was the first who used the name *Cambarus* as a generic name, and proposed a subdivision of the genus into three groups based on the structure of the rostrum and the first pleopod of the male.

"First group: Rostrum subquadrangularly elongated, terminated anteriorly by three conical and acute spines, the two lateral smaller than the middle one, which forms the tip. Extremity of the anterior pair of abdominal legs (in the male) straight and acute." (Girard 1852: 87).

"Second group: Rostrum generally broad, conical and short, with margins entire and toothless, terminated anteriorly by an acute and comparatively short point. Anterior pair of abdominal legs (in the male) recurved on their extremity, the tip of which is rounded." (Girard 1852: 88).

"Third group: Rostrum very much elongated, conical, tapering, provided on both sides and rather near the extremity with a small and acute spine, sometimes, however, but very slightly developed." (Girard 1852: 91).

Hagen's Monograph (1870) includes a discussion of 32 species of *Cambarus* which he divided into three groups:

Group I: (Type, *C. acutus*) "The third and the fourth pair of legs of the males hooked; rostrum triangular, elongated, with an ante-apical tooth each side, at least in the young; first pair of abdominal legs with the exterior part truncated at the tip with several somewhat dilated incurved corneous teeth, occasionally covered with a pencil of hairs; the interior part terminated in a short, acute, and for the most part outwardly directed spine." (Hagen 1870: 32).

Group II: (Type, *C. affinis* [=synonym of *limosus*]) "The third legs of the males hooked; rostrum subquadrangularly elongated, with an antepical tooth on each side, at least in the young; first pair of abdominal legs bifid, elongated, straight and acute at tip." (Hagen 1870: 57).

Group III: (Type, *C. bartonii*) "The third legs of the male hooked; rostrum short, toothless; first pair of abdominal legs with the tip of the exterior part recurved, the tip of the interior part short." (Hagen 1870: 74).

In 1872 Cope described *Orconectes inermis* from Wyandotte Cave.<sup>1</sup>

In Faxon's Revision of the Astacidae (1885), he divided the genus *Cambarus* into five groups based upon somewhat the same characters as were used by Hagen.

Group I: (Type, *C. blandingii*) "Third segment of third and fourth pairs of legs of male hooked. First pair of abdominal appendages of male with outer part truncate at the tip, and furnished with one to three small recurved teeth; inner part terminated by a short acute spine, which is generally directed outwards." (Faxon 1885: 17).

Group II: (Type, *C. advena*) "Third segment of third pair of legs of male hooked. First pair of abdominal legs of male similar to those of Group I." (Faxon 1885: 47).

Group III: (Type, *C. bartonii*) "Third segment of third pair of legs hooked. First

1 Mr. Leslie Hubricht of the St. Louis Botanical Garden has kindly lent me specimens from Siebert's Well Cave, and has informed me that Cope took his specimens from this Cave which is just below Wyandotte Cave, and that the latter had no standing water in it except small drip pools.



pair of abdominal appendages of the male thick, the inner and outer parts each terminating in a short recurved tooth." (Faxon 1885: 59).

Group IV: (Type, *C. affinis* = synonym of *limosus*) "Third segment of third pair of legs of the male hooked. First abdominal appendages of the male bifid, terminated by two nearly straight styliform branches." (Faxon 1885: 85).

Group V: (Type, *C. montezumae*) "Third segment of the second and third pairs of legs hooked. First pair of abdominal appendages of the male similar to those of the species included in Group IV." (Faxon 1885: 121).

Thus Faxon recognized the groups set up by Hagen; however, he split his Group II from Hagen's Group I, and in addition established his Group V as new.

Faxon (1898: 644) listed *Astacus bartonii* Fabricius as the type of the genus *Cambarus*.

In 1905 Ortmann erected four subgenera of the genus *Cambarus*. They are as follows:

Subgenus *Cambarus*: (Type, *C. blandingii*) "Sexual organs of male stout, more or less straight, and comparatively short, truncated or blunt at the tip, the outer part ending in 1-3 horny teeth, which are sometimes recurved, or compressed, or plate-like, and are always sharply distinguishable from the blunt end. Inner part terminated by a shorter or longer, acute spine, which is sometimes distinct from the tip of this part, so that it appears two-pointed. In the male the third or the third and fourth pereiopods have hooks." (Ortmann 1905: 97)

Subgenus *Cambarellus*: (Type, *C. montezumae*) "Sexual organs of male stout, straight, or slightly curved at the tips. Outer part ending in two horny teeth, which are rather long, taper rapidly, and are not sharply distinguishable from the end, which is not truncated. Inner part terminated by a rather long, acute spine. In the male, the second and third pereiopods have hooks." (Ortmann 1905: 97)

Subgenus *Faxonius*: (Type, *C. limosus*) "Sexual organs of male shorter or longer, not very stout, generally slender, or with slightly curved tips. Tips never truncated, ending always in two more or less elongated spines, the one formed by the outer part, and horny, the other formed by the inner part and softer. There is never more than one tip to the outer part, and there is no terminal tooth distinguishable, but the tip tapers gradually, or the whole outer part is setiform. In the male generally the third pereiopods only have hooks, very rarely (in *pellucidus*) hooks are found on third and fourth pereiopods." (Ortmann 1905: 97)

Subgenus *Bartoniis*: (Type, *C. bartonii*) "Sexual organs of male very uniform throughout the subgenus. They are short and thick, inner and outer parts each terminating in only one short and thick spine, tapering to a point. Both terminal spines are strongly recurved, forming with the basal part about a right angle. In the male, only the third pereiopods possess hooks." (Ortmann 1905: 97)

In a second paper published by Ortmann during 1905 he described a fifth subgenus, removing his section of *Cambarus digueti* from the subgenus *Cambarus*.

Subgenus *Procambarus*: (Type, *C. digueti*) "Sexual organs of male stout, more or less straight and comparatively short, rather blunt at the end, but not truncate. The two parts in close opposition up to the tips. The outer one ending bluntly, without horny teeth; the inner one being more or less similar to the outer one, but possessing in various positions one horny spine. Anterior margin with a shoulder near the tips. In the male the third pereiopods have hooks." (Ortmann 1905b: 437)

In 1906 Ortmann described his sixth and only monotypic subgenus, *Paracambarus*, of which *paradoxus* is the type.

Subgenus *Paracambarus*: (Type, *C. paradoxus*) "Sexual organs of male with the two parts in close apposition to their tips; in the male of the first form, both tips are shortly pointed and horny; in addition there is, on the posterior margin of the inner part, at a short distance from the tip, a long and strong, horny spine. Anterior margin of sexual organs without shoulder. Male with hooks on the ischiopodite of fourth pereopods only. Female with a spiniform process on the sternum between the fifth pereopods." (Ortmann 1906: 1)

In 1911 Fowler published a report on the Crustacea of New Jersey, in which he proposed the name *Ortmannicus* to replace Ortmann's *Cambarus*. Because the typical species of the genus *Cambarus* is *C. bartonii* (designated by Faxon in 1898), and because the typical subgenus must include that species, Fowler synonymized Ortmann's *Bartoni* with *Cambarus*.

"*Ortmannicus* is here proposed as a new subgeneric name, the intended *Bartoni* Ortmann being an exact synonym of *Cambarus*. *Ortmannicus* will thus embrace the limits as defined by *Bartoni*. This is offered as a slight tribute to Dr. Ortmann's recent studies of the crawfishes, which are among the most important and comprehensive yet attempted."<sup>2</sup> (Fowler 1911: 341)

In 1914, Faxon, refusing to follow Ortmann's use of subgeneric categories, proposed the following:

Group I (= *Procambarus* Ortmann).

Group II (= *Cambarus* Ortmann, in part.) This group included those species of Ortmann's *Cambarus* having hooks on the ischiopodites of only the third pereopods in the male.

Group III (*Cambarus* Ortmann, in part.) This group included those species of Ortmann's *Cambarus* having hooks on the ischiopodites of both the third and fourth pereopods in the male.

Group IV (*Paracambarus* Ortmann).

Group V (*Cambarellus* Ortmann).

Group VI (*Faxonius* Ortmann).

Group VII (*Bartoni* Ortmann).

Creaser (1933) adopted the use of *Faxonius* as a generic name, and proposed a new subgenus of *Faxonius*, *Faxonella*, to include *Faxonius clypeatus*. "In view of the peculiarities of the sexual appendage with one long ramus and one short one, I deem this species worthy of subgeneric ranking and designate it *Faxonella*, new subgenus of *Faxonius*." (Creaser 1933: 21)

In 1938 Lyle introduced the subgeneric name *Girardiella* to include those species Faxon had referred to his Group II.

<sup>2</sup> It is quite obvious here that when Fowler states "*Ortmannicus* will thus embrace the limits as defined by *Bartoni*" that this is not what he means. Fortunately he selected a type, *C. blandingii*, for *Ortmannicus*, thus saving this name from also being a synonym of *Cambarus*. Fowler's sentence should read "*Ortmannicus* will thus embrace the limits as defined by Ortmann's *Cambarus*."

In the light of the foregoing historical consideration and eight years' study of several thousand crayfish specimens, (principally from the southern states and Mexico, but including the types in the United States National Museum, the Museum of Comparative Zoology, and the Philadelphia Academy of Natural Sciences) I wish to propose the new classification presented on page 339. This is followed by definitions of the subfamilies of the Astacidae, and a key to the genera of the second of these subfamilies, the Cambarinae, is included. Under this subfamily I introduce some remarks on the significance of generic characters which are used in the definition and classification of crayfishes.

#### Family ASTACIDAE

Subfamily I. ASTACINAE, comprising the crayfishes of North America west of the Rocky Mountains, Europe, and Asia. "In these the first abdominal somite in the male bears a pair of styliform appendages; [The first abdominal appendages are rudimentary or absent in the female] the podobranchiae borne on the second and third maxillipeds and on the first three pairs of legs are furnished with a broad bilobed plaited lamina; the epipodite of the first maxilliped is destitute of branchial filaments; the coxopoditic setae are acute, not hooked, at the end; the telson is commonly divided more or less completely by a transverse suture." A pair of branchiae present "on the wall of the last thoracic somite, and a folded lamina on the podobranchiae of the thoracic appendages from the second maxilliped to the penultimate pair of legs inclusive." (Faxon 1885: 2)

Subfamily II. CAMBARINAE, comprising the crayfishes of North America east of the Rocky Mountains with one exception.<sup>4</sup> Characters as in Astacinae except that gills are absent from the last thoracic somite, and there is no bilobed lamina on the podobranchiae of the penultimate pair of legs.

#### Subfamily CAMBARINAE

It is impossible to designate a group of characters which are invariably indicative of the generic status of all species. I wish to point out the untrustworthiness of certain characters hitherto relied upon to such an extent that species which are closely related have been referred to separate groups or subgenera.

Faxon, adhering to the idea that the hooks on the ischiopodites of the third or third and fourth pereopods were a "sine qua non" in determining relationships, insisted even in his last paper (1914) that there were two distinct groups (his Groups II and III) in Ortmann's subgenus *Cambarus* [= synonym of *Procambarus*]. He even went so far as to remove *C. pellucidus* from all of the rest of its relatives, both geographically and otherwise, and place it in his Group III, simply because it bore hooks on the third and fourth pereopods. With the subsequent discovery of new species of *Procambarus*, and examination

<sup>4</sup> *Cambarus clarkii* has been introduced into California, and Dr. Waldo L. Schmitt of the United States National Museum has informed me that it has become well established in the southern part of that state.

Summary of the Generic and Subgeneric Changes (1870 - 1941)<sup>3</sup>

Hagen 1870	Faxon 1885	Ottmann 1905-6	Fowler 1911	Faxon 1914	Creaser 1933	Lyle 1938	Generic Names recognized in the present paper.
Group III, in part		<i>Procambarus</i>	<i>Procambarus</i>	Group I			
Group III, in part	Group I			Group II		<i>Citardicella</i>	<i>Procambarus</i>
Group I, in part	Group II	<i>Cambarus</i>	<i>Ortmannicus</i>	Group III			
		<i>Paracambarus</i>	<i>Paracambarus</i>	Group IV			<i>Paracambarus</i>
	Group V	<i>Cambarcellus</i>	<i>Cambarellus</i>	Group V			<i>Cambarellus</i>
Group II	Group IV	<i>Faxonius</i>	<i>Faxonius</i>	Group VI	<i>Faxonius</i> , as a generic name.		<i>Oreonectes</i>
Group III, in part	Group III	<i>Barlonius</i>	<i>Cambarus</i>	Group VII			<i>Cambarus</i>
							<i>Troglocambarus</i>

<sup>3</sup> Because of the difficulty in arranging Girard's subdivision to fit this chart, and its lack of value in the present treatment, I have intentionally omitted it.

of many specimens of species which were already known, I have gathered considerable evidence indicating that a division of this sort (i.e. based on the hooks on the ischiopodites of the pereiopods) is highly unnatural and gives one a very distorted conception of the group as a whole. This character, though in general a fairly good one, is variable not only in the groups but even in the individual species. In a new and as yet undescribed species very closely related to *Procambarus advena*, hooks are present on the ischiopodites of the third and fourth pereiopods while *advena* bears hooks only on those of the third pereiopods. *P. alleni* has its affinities with the members of Faxon's Group II, but if we follow Faxon, it must be referred to his Group III because it has hooks on the ischiopodites of the third and fourth pereiopods. The same is true for *P. kilbyi* and *P. barbatus*, as well as for several as yet undescribed species which present the same difficulty, i.e. these have their closest affinities with the members of Faxon's Group II but because they have hooks on the ischiopodites of the third and fourth pereiopods they must be referred to Faxon's Group III.

The above paragraph points out some of the instances where the value of this character breaks down. On the other hand there are many instances where this character is of extreme value. All of the members of the genus *Cambarellus* have hooks on the ischiopodites of the second and third pereiopods. *Paracambarus paradoxus*, the only species of the genus, has hooks present on the ischiopodite of the fourth pereiopod only. While the presence of hooks only on the third pereiopods is not peculiar to the genus *Cambarus*, all of its members possess it. Hence, we cannot neglect this character but at the same time it must be used with discretion.

With little doubt the structure of the first pleopod of the first form male is the most reliable feature on which to base our ideas of relationships. Here it is the number and arrangement of the terminal processes which seem to lend themselves to such a study. It has been my experience that the arrangement may in some instances mean more than actual number of terminals; for example, should the number of terminal processes in *Procambarus spiculifer* and *Cambarellus montezumae* be compared, it would be found to be identical; even the same process is missing in both of them (Hobbs 1941b); however, when the arrangements, proportionate sizes, and general conformations are studied it is seen that these two species are only distantly related.

For certain related groups the annulus ventralis of the female shows, in its configurations, degrees of variation within certain limits. Considerable investigation of this structure would probably result in its being used, at least to a certain extent, as a generic character. As things now stand, an isolated female which does not belong to a species that is very familiar to the taxonomist, generally goes unnamed, and often cannot be determined to genus.

In 1885 Faxon was aware of the fact that Girard's subdivision of the genus *Cambarus* was untenable because it would "divorce species which in the totality of their organization are most closely related" (Faxon 1885: 16). As has been observed from the statements above, I have this same feeling concerning Faxon's proposals, and I do not doubt that with the further discovery of new species

and a more thorough investigation of those already known that the proposals I am making in this paper will to some extent be objected to on the same grounds.

I am introducing two generic characters in the diagnosis of *Troglocambarus* which have never before been appealed to, probably for the simple reason that, so far as I know, other crayfish do not exhibit these characters. The maxillipeds are tremendously enlarged, and on the inner margin of the ischiopodite of this appendage there are no teeth.

KEY TO THE GENERA OF THE SUBFAMILY CAMBARINAE  
(Based on the First Form Male)

- |       |  |                   |
|-------|--|-------------------|
| 1     | First pleopod of first form male terminating in three or more distinct parts, or two distinct parts, plus a strong shoulder on the cephalic margin near the tip (See Plate 3, Figs. 6, 7 and 11) | 2                 |
| 1'    | First pleopod of first form male terminating in only two distinct parts; never with a well developed shoulder on the cephalic margin near the tip (See Plate 3, Figs. 1, 3 and 10)               | 5                 |
| 2(1)  | Ischiopodite of third maxillipeds with teeth along inner margin  | 3                 |
| 2'    | Ischiopodite of third maxillipeds without teeth along inner margin.... <i>Troglocambarus</i>   |                   |
| 3(2)  | Hooks present on the ischiopodites of the second and third or third and fourth or only the third pereopods; never only on the fourth   | 4                 |
| 3'    | Hooks present only on the ischiopodites of the fourth pereopods.... <i>Paracambarus</i>  |                   |
| 4(3)  | Hooks present on the ischiopodites of the third or third and fourth pereopods; never on the second pereopods.... <i>Procambarus</i>  |                   |
| 4'    | Hooks present on the ischiopodites of the second and third pereopods.... <i>Cambarellus</i>  |                   |
| 5(1') | Two terminals on first pleopod generally short and strongly recurved. Entire appendage short and heavy   | <i>Cambarus</i>   |
| 5'    | Terminals on first pleopod short or long; never strongly recurved; if recurved, they are slender and in most cases setiform  | <i>Orconectes</i> |

Genus PROCAMBARUS Ortmann 1905b: 437

Type, here designated *Cambarus digueti* Bouvier.

In 1911 Fowler proposed the name *Ortmannicus* as a subgeneric name to replace the name *Cambarus* used by Ortmann (See pp. 337, 339). Both in 1885 and in 1914, Faxon split this group into two parts which he termed his groups II and III. Both Faxon and Ortmann recognized the assemblage of species referred to by the latter as *Procambarus* as a distinct group.

I have already pointed out that Faxon's groups II and III are very artificial and should not be recognized. I am also unwilling to admit the uniqueness of the characters of *Procambarus* pointed out by Ortmann and Faxon. It seems to me that the members of the *gracilis* and *simulans* groups have considerably more in common with the *digueti* group than with most of the other species of the subgenus *Ortmannicus* (sens. strict.). Ortmann (1905b) in his description of the subgenus *Procambarus* was of the opinion that his *gracilis* and *simulans* sections were more nearly related to the *blandingii* section of his subgenus *Cambarus* than to the members of *Procambarus*. On this point I do

not agree with him, for if the pleopods of the males are compared it is readily seen that all of the species he referred to the *gracilis* and *simulans* sections (except *advena*) along with *alleni* and several others bear the "shoulder" he emphasized, and that their tips are not markedly different from those of the species referred to *Procambarus*. Therefore I propose that the subgenus *Ortmanmanicus* Fowler (of which *Cambarus* Ortmann is a synonym) and the subgenus *Procambarus* Ortmann both be referred to a single genus, *Procambarus*. I am proposing no subgenera in this genus.

*Diagnosis*.—First pleopod of first form male terminating in from two to five distinct parts which may be truncate, plate-like or spiniform. Shoulders present or absent on cephalic surface of distal third. If the pleopod terminates in only two parts this shoulder is always present. Hooks present on the ischiopodites of the third or of the third and fourth pereopods in the male. Third maxillipeds of normal size bearing a row of teeth along the inner margin of the ischiopodite.

Thus this genus will include groups I, II, and III of Faxon (1914) (excluding *Cambarus pellucidus*, which is placed in the genus *Orconectes*) and in addition the following species which have been described since 1914.

#### PROCAMBARUS BLANDINGII CUEVACHICAE (Hobbs)

*Cambarus blandingii cuevachicae* Hobbs, Zoologica, 1941, 26, Part I, (1):1-4, 1 text-fig.

*Type Locality*.—La Cueva Chica, a limestone cave, about 1 mile northeast of Pujal, San Luis Potosi, Mexico. *Holotype*, U.S.N.M., No. 80030 (1 ♂, form I); *Allotype*, U.S.N.M., No. 80030 (1 ♀); *Paratypes*: U.S.N.M. (1 ♂, form II); Peabody Museum (1 ♂, form I, 7 ♂♂, form II, 10 ♀♀, 4 immature ♂♂, 6 immature ♀♀); Personal Collection, Univ. of Fla. (1 ♂, form I, 1 ♂, form II, 1 ♀).

#### PROCAMBARUS CONTRERASI (Creaser)

*Cambarus contrerasi* Creaser, Occ. Pap. M.M.Z., 1931, No. 224, pp. 1-4, 2 pls.

*Type Locality*.—Tributary of the Rio Cazones near Agua Fria, 12 miles south of Miahupan, State of Puebla, Mexico. *Type*, M.M.Z., No. 53262 (1 ♂, form I); *Paratype*, U.S.N.M. (1 ♂, form II).

#### PROCAMBARUS HUBBELLII (Hobbs)

*Cambarus hubbellii* Hobbs, Proc. U. S. Nat. Mus., 1940, 89(3097):406-410, 1 fig.

*Type Locality*.—A roadside ditch in the flatwoods 1 mile east of Bonifay, Holmes County, Florida, on St. Highway No. 1. *Holotype*, U.S.N.M., No. 76593 (1 ♂, form I); *Allotype*, U.S.N.M. (1 ♀); *Paratypes*: U.S.N.M. (1 ♂, form II); M.C.Z. (1 ♂, form I, 1 ♂, form II, 1 ♀); M.M.Z. (1 ♂, form I, 1 ♂, form II, 1 ♀); Charleston Museum (1 ♂, form I, 1 ♂, form II, 1 ♀); Personal Collection, Univ. of Fla. (6 ♂♂, form I, 12 ♂♂, form II, 24 ♀♀, 29 immature ♂♂, 41 immature ♀♀).



## PROCAMBARUS KILBYI (Hobbs)

*Cambarus kilbyi* Hobbs, Proc. U. S. Nat. Mus., 1940, 89(3097):410-414, 1 fig.

*Type Locality*.—A small creek about 7 miles northwest of Blountstown, Calhoun County, Florida, on St. Highway No. 6. *Holotype* U.S.N.M. No. 76594 (1♂, form I); *Allotype*, U.S.N.M. (1♀); *Paratypes*: U.S.N.M. (1♂, form II); M.C.Z. (1♂, form I, 1♂, form II, 1♀); M.M.Z. (1♂, form I, 1♂, form II, 1♀); Personal Collection, Univ. of Fla. (5♂♂, form I, 10♂♂, form II, 5♀♀, 37 immature ♂♂, 43 immature ♀♀).

## PROCAMBARUS LUCIFUGUS ALACHUA (Hobbs)

*Cambarus lucifugus alachua* Hobbs, Proc. U. S. Nat. Mus., 1940, 89(3097):402-406, 1 fig.

*Type Locality*.—A small cave, Hog Sink, about 10 miles west of Gainesville, Alachua County, Florida. *Holotype*, U.S.N.M., No. 76592 (1♂, form I); *Allotype*, U.S.N.M., No. 76592 (1♀); *Paratypes*: U.S.N.M. (1♂, form II); M.M.Z. (1♂, form II, 1♀); Personal Collection, Univ. of Fla. (1♂, form I, 18♀♀, 9 immature ♂♂, 20 immature ♀♀).

## PROCAMBARUS LUCIFUGUS LUCIFUGUS (Hobbs)

*Cambarus lucifugus lucifugus* Hobbs, Proc. U. S. Nat. Mus. 1940, 89(3097):398-402, 1 fig.

*Type Locality*.—Gum Cave, about 5 miles southwest of Floral City, Citrus County, Florida. *Holotype*, U.S.N.M., No. 77916 (1♂, form I); *Allotype*, U.S.N.M., No. 77918 (1♀); *Paratypes*: U.S.N.M., No. 77917 (1♂, form II); M.C.Z. (1♂, form I, 1♀); M.M.Z. (1♂, form I, 1♀); Personal Collection, Univ. of Fla. (8♂♂, form I, 18♀♀, 2 immature ♂♂, 1 immature ♀).

## PROCAMBARUS LUNZI (Hobbs)

*Cambarus lunzi* Hobbs, Charleston Mus. Leaflet. 1940, (14):3-7, 1 pl.

*Type Locality*.—Roadside ditch in the flatwoods, 1.4 miles southeast of Early Branch on St. Highway No. 28, Hampton County, South Carolina. *Holotype* and *Allotype*, U.S.N.M., No. 79301 (1♂, form I, 1♀).

## PROCAMBARUS PALLIDUS (Hobbs)

*Cambarus pallidus* Hobbs, Proc. U. S. Nat. Mus., 1940, 89(3097):394-398, 1 fig.

*Type Locality*.—Warrens Cave, 11 miles northwest of Gainesville, Alachua County, Florida. *Holotype*, U.S.N.M., No. 76591 (1♂, form I); *Allotype*, U.S.N.M., No. 76591 (1♀); *Paratypes*: U.S.N.M. (1♂, form II); M.C.Z. (1♀); M.M.Z. (1♀); Personal Collection, Univ. of Fla. (1♂, form I, 3♂♂, form II, 6♀♀).

## PROCAMBARUS PEARSEI (Creaser)

*Cambarus pearsei* Creaser, Occ. Pap. M. M. Z., 1934, No. 285, pp. 1-4, 1 fig.

*Type Locality*.—Pond and ditch on Highway No. 22, south of Fayette-

ville, Cumberland County, North Carolina. *Holotype*, M.M.Z., No. 53792 (1♂, form I); *Allotype*, M.M.Z., No. 53793 (1♀); *Paratypes*: U.S.N.M., (1♂, 1♀); M.M.Z., No. 53794 (a number of specimens).

PROCAMBARUS PICTUS (Hobbs)

*Cambarus pictus* Hobbs, Proc. U. S. Nat. Mus., 1940, 89(3097):419-422, 1 fig.

*Type Locality*.—A small, swift swamp stream about 2 miles southwest of Green Cove Springs, Clay County, Florida, on St. Highway No. 48. *Holotype*, U.S.N.M., No. 76596 (1♂, form I); *Allotype*, U.S.N.M., No. 76596 (1♀); *Paratypes*: U.S.N.M. (1♂, form II); M.C.Z. (1♂, form I, 1♂, form II, 1♀); M.M.Z. (1♂, form I, 1♀); Personal Collection, Univ. of Fla. (5♂♂, form I, 1♂, form II, 5♀♀).

PROCAMBARUS RATHBUNAE (Hobbs)

*Cambarus rathbunae* Hobbs, Proc. U. S. Nat. Mus., 1940, 89(3097):414-418, 1 fig.

*Type Locality*.—Near the Yellow River at Milligan, Okaloosa County, Florida, at intersection of St. Highway No. 41 and U.S. Highway No. 90. *Holotype*, U.S.N.M., No. 76595 (1♂, form I); *Allotype*, U.S.N.M. (1♀); *Paratypes*: U.S.N.M. (1♂, form II); M.C.Z. (1♂, form II, 1♀); M.M.Z. (1♂, form II, 1♀); Personal Collection, Univ. of Fla. (1♂, form I, 2♂♂, form II, and 6♀♀).

PROCAMBARUS ROGERSI (Hobbs)

*Cambarus rogersi* Hobbs, Proc. Wash. Acad. Sci., 1938, 28(2):61-65, 1 pl.

*Type Locality*.—Low pine flatwoods 4 miles north of Blountstown, Calhoun County, Florida, on St. Highway No. 6. *Holotype*, U.S.N.M., No. 75120 (1♂, form I); *Allotype*, U.S.N.M., No. 75121 (1♀); *Paratypes*: U.S.N.M. (1♂, form II); M.M.Z. (1♂, form I, 1♀); M.C.Z. (1♂, form I, 1♀); Carnegie Mus. (1♂, form I, 1♀); Personal Collection, Univ. of Fla. (4♂♂, form I, 2♂♂, form II, 3♀♀).

Genus PARACAMBARUS Ortmann 1906: 1

Type, by monotypy, *Cambarus paradoxus* Ortmann.

*Diagnosis*.—First pleopod of first form male terminating in three distinct parts; the mesial process is long and heavy and is bent caudad at about a 60 degree angle with the main shaft of the appendage; the cephalic process is small and hood-like partially covering the central projection, the latter being somewhat beak-like; a rudiment of the caudal process may be seen near the tip of the appendage if viewed laterally. No shoulder present on anterior margin of appendage. Male with hooks on the ischiopodites of the fourth pereopods only. Third maxilliped of normal size bearing a row of teeth along the inner margin of the ischiopodite.

Genus *Troglocambarus*, new genus

Monotypic: type, here designated, *Troglocambarus macleani* new sp.

*Diagnosis*.—First pleopod of first form male terminating in four distinct parts; the mesial and cephalic processes are somewhat spiniform and non-corneous; the caudal process and central projection are corneous and somewhat blade-like, the latter terminating in a rather sharp point. The eyes reduced and without pigment. The third maxilliped is tremendously enlarged, the ischiopodite of which bears no teeth along the inner margin. The species is rather small and in life almost transparent.

*Holotypic Male* (Form I).—Body in cross section subovate, compressed laterally. Width of thorax greater than width of abdomen (.70-.50 cm.).

Width of carapace slightly greater than height (.70-.68). Greatest width of carapace slightly cephalad of caudodorsal margin of cervical groove.

Areola of moderate width, about 3.54 times as long as wide. Length of areola 37.9% of entire length of carapace.

Rostrum short, not reaching distal end of basal segment of antennule; concave above, sides convergent. No lateral spines. Postorbital ridges gradually merge into the carapace cephalad, terminating in neither a tubercle nor spine. Subrostral ridge evident in dorsal view along proximal half of rostrum.

Surface of carapace smooth and polished. No lateral spines present. Branchiostegal spines absent, replaced by a small tubercle. Suborbital angle absent.

Abdomen longer than thorax. Anterior section of telson with one spine in each posterolateral corner.

Epistome sub-minarette shaped, surface excavate.

Antennules much elongate, no spine present on ventral surface of basal segment.

Antennae twice as long as body. Antennal scales broad, broadest in middle. Spine on outer distal margin weak, extending almost to distal end of second segment of peduncle of antennule.

Third maxillipeds tremendously enlarged, extend cephalad far beyond peduncles of antennae or antennules, reaching distal end of carpus of chela when both are extended. Ischiopodite bears no teeth on inner margin, but instead a row of rather strong setae; however, apparently not stronger than the setae elsewhere on the appendage.

First pereiopod long and slender; merus, propus, and carapace subequal in length. Palm of chelae subcylindrically smooth, bearing no tubercles or ridges; however, studded with a few scattered setae. *Immovable finger* with three minute tubercles along basal seventh of upper surface of mesial margin. A short distance distad of the distal one a slightly larger tubercle extends mesiad from the lower mesial margin. Several crowded rows of minute plumose setae extend along the entire mesial margin of the finger. A single widely spaced row of large setae extends along the lower lateral surface of the finger. *Movable*

*finger* with two minute tubercles along basal seventh of lower surface of lateral margin. Several rows of minute plumose setae extend along the entire lateral margin of the finger. A single widely spaced row of large setae extends along the lower mesial surface of the finger. *Carpus* longer than broad, smooth and polished, no longitudinal furrow above. Merus with a row of 32 spines on upper surface. Lower surface with a median row of 34 spines, a lateral row of nine tubercles or spines, a medial row of 10 tubercles or spines. All three of these run together proximad so that there are no well-defined limits between them. Ischiopodites of third and fourth pereiopods with hooks, both hooks simple.

First pleopod extending cephalad to coxopodite of third pereiopod. Tips terminating in four distinct parts, all of which are bent caudad. Mesial process long, spiculiform, directed caudolaterad. Cephalic process spiniform and arises from the cephalic margin, bent caudad and extends somewhat mesiad of the central projection. Caudal process, corneous, blade-like, and very conspicuous, extends caudad from the caudolateral portion of the tip of the appendage. Central projection corneous and acute, is directed caudad.

*Female Allotype*.—Besides a slight difference in number of tubercles in various parts, the female differs from the holotypic male in the following points: Differences may be seen in the proportion of length of the palm of the hand to the length of the movable finger in the two sexes. Rostrum more rounded and less acute; right margin with a slight angle at base of acumen. Epistome more triangular. Annulus ventralis: Cephalic portion of the annulus ventralis hidden beneath a somewhat flattened plate-like shelf arising from the seventh thoracic sternite between the third and fourth pereiopods and extending caudad to the caudal margin of the coxopodites of the fourth pereiopods. The plate is deeply cleft caudad along the midventral line. The annulus is sub-elliptical with the transverse axis the longer. The sinus originates beneath the sinistral underhanging shelf, curves gently dextrad so that it may be seen beneath the margins of the cleft in the underhanging shelf; here it does not quite reach the midventral line before it turns caudosinistrad; extends sinistrad of the sinistral side of the cleft and caudad of the caudal margin of the shelf. At this point it turns rather abruptly dextrad, crosses the midventral line and swings caudad and then caudosinistrad to the caudal margin of the annulus, reaching it on about the midventral line.

*Paratypic Male (Form II)*.—Differing only slightly from the male of the first form. Hooks on the ischiopodites of the third and fourth pereiopods much reduced; the epistome slightly broader and shorter. The first pleopod exhibits a marked reduction in the caudal process. Here it is represented by a slight projection lying mesiad and somewhat under the centro-caudal process. None of the processes are corneous and all are blunter.

*Measurements*.—The holotype: Carapace, height 0.68, width 0.70, length 1.40 cm.; areola, width 0.15, length 0.53 cm.; rostrum, length 0.23, width 0.17 cm.; abdomen, length 1.73, width 0.50 cm.; right chela, inner margin of palm 0.58, width of palm 0.19, length of outer margin of hand 1.36, length of movable finger 0.74 cm. Flagellum of antennae approximately 6.00 cm. The

allotype: Carapace, height 0.66, width 0.69, length 1.30 cm.; areola, width 0.13, length 0.50 cm.; rostrum, length 0.19, width 0.18 cm.; abdomen, length 1.64, width 0.50 cm.; right chela, inner margin of palm 0.42, width of palm 0.14, length of outer margin of hand 1.17, length of movable finger 0.72 cm. Flagellum of antennae approximately 6.00 cm.

*Type Locality*.—"Squirrel Chimney," a small cave about 11 miles northwest of Gainesville, Alachua County, Florida (Sec. 21, Twp. 9S, R. 18E). Squirrel Chimney, as its name indicates, is a circular solution cavity with almost vertical walls, the latter supporting a luxuriant growth of liverworts, mosses, and small ferns. This "chimney" penetrates the surface soil and limestone to a depth of approximately 50 feet where it strikes the water table. Debris has fallen into the sink and has accumulated at the water level so that a little less

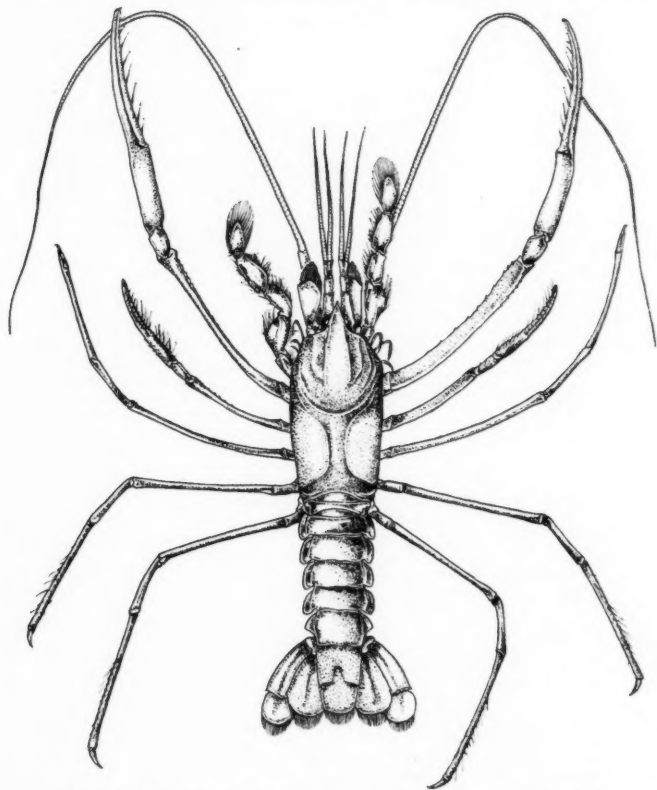


Plate 1.—Dorsal View of *Troglocambarus maclanei*, male, form I.

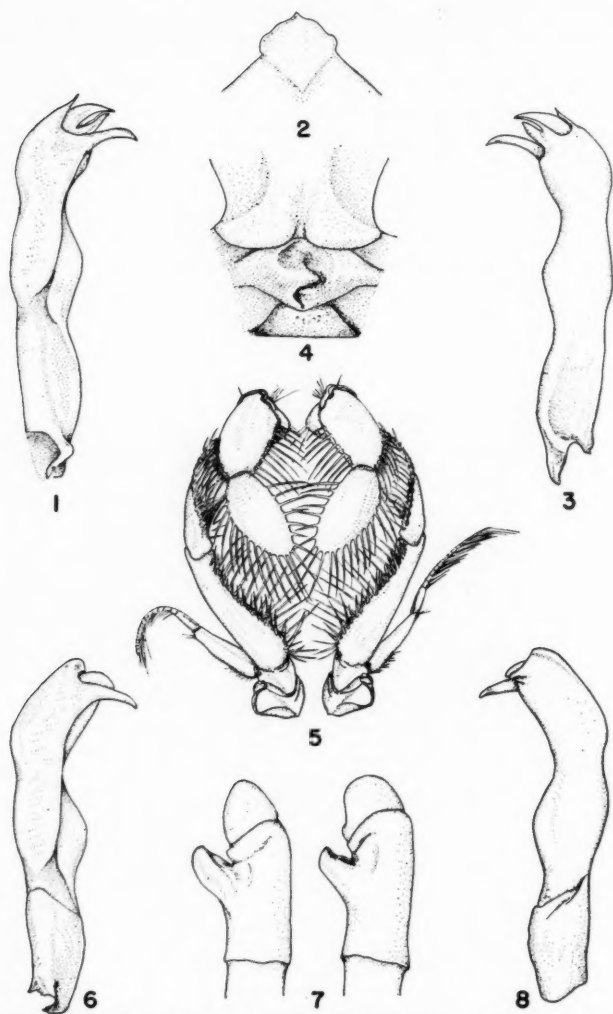


PLATE 2.—*Troglacambarus maclanei*. Fig. 1. Mesial view of first pleopod of male, form I. Fig. 2. Epistome. Fig. 3. Lateral view of first pleopod of male, form I. Fig. 4. Annulus ventralis and adjacent portion of the sternum, female. Fig. 5. Cephalo-ventral view of position of third maxillipeds. Fig. 6. Mesial view of first pleopod of male, form II. Fig. 7. Ischiopodites of third and fourth pereiopods, male, form I. Fig. 8. Lateral view of first pleopod of male, form II. Pubescence has been removed from all structures illustrated except Fig. 5.

than half of the opening contains water, the rest of it being covered over with fallen leaves which are supported by dead tree trunks and limbs. Within six to eight feet of the bottom a small opening about three feet in diameter leads out into a fissure about 25 yards long and four feet wide, the whole bottom of which is filled with water ranging in depth from a few inches to 30 feet at the deepest place sounded. The light is very dim inside of the fissure, even at the opening, and a short distance away, to the eye it is completely dark. The water is very clear; however, the surface film sometimes supports a coat of fine silt and debris. The bottom consists of mud, sand, and silt with large limerock outcrops.

*Habits.*—The first specimen of this species was collected on March 19, 1941, by Mr. William A. McLane<sup>5</sup> from the shallow portion of this fissure pool in Squirrel Chimney. The specimen was resting on the mud bottom. It is worthy of note that for the past six or seven years I have been visiting the caves from which *T. maclanei* has been taken, and until March 19, 1941, I had never taken a specimen, while I have collected numerous specimens of *Procambarus pallidus*, *Lucifugus lucifugus*, and *Lucifugus alachua* from them.

The following data have been given me by Mr. Lewis J. Marchand, who collected all of my 23 additional specimens; although I was with Mr. Marchand when the specimens were taken, he actually caught all of them. The crayfish are always found in the shallower portions of the pool, where they cling bottom-side-up to the limestone roof where it dips below the water table. Of the 24 specimens taken only three were found on the bottom, the rest clinging to the submerged ceiling. Two or three of the specimens were taken from open water as they released their hold on the ceiling or were jarred loose, and floated toward the bottom. To collect most of the specimens it was necessary for Mr. Marchand to dive below the surface and explore the submerged ceilings, and in some instances to go horizontally beneath these ceilings as much as 15 feet. To facilitate such a method of collecting a headlight and water-goggles were used. Mr. Marchand found that *T. maclanei* could be taken readily by hand, whereas it is almost impossible to catch the larger cave species without a dip net.

It is to be emphasized that *T. maclanei* does not occur abundantly in these caves. A total of 24 specimens were taken as the result of approximately 18 hours spent in the water in diligent search for this crayfish. In Squirrel Chimney, where *maclanei* is most common, it is about 1/20 as numerous as *P. pallidus*.

That *T. maclanei* is at least occasionally cannibalistic was evinced by the capture of one specimen which was in the process of devouring a slightly smaller one.

Clinging to the ventral surface of these crayfish were octracods and

<sup>5</sup> It is a pleasure to name this species for Mr. McLane, who has been a companion on many collecting trips, and who has added numerous valuable specimens to my collection.



branchiobdellids, *Cambarincola philadelphia* and *C. vitrea*.<sup>6</sup> These annelids were observed in the gill chambers of live crayfish, in which the carapace is so transparent that the pulsating movements of the worm's circulatory system could be seen easily.

*Disposition of Types*.—The hototypic male, form I, the allotypic female, and a paratypic male, form II, are deposited in the U.S.N.M. (Nos. 79385, 79386, 79387). Of the remaining paratypes, one male, form I, and a female are deposited in the Museum of Comparative Zoology; one male, form I, in the University of Michigan Museum of Zoology; one male, form I, two males, form II, one female, and two immature specimens are retained in my personal collection.

*Distribution*.—*Troglocambarus maclanei* has been taken from three caves in Florida: Squirrel Chimney (the type locality), 11 miles northwest of Gainesville; Goat Sink, 12 miles northwest of Gainesville (both localities in Alachua County); and Gum Cave, about five miles southwest of Floral City, Citrus County, Florida.

*Relationships*.—This new species has more characters in common with the members of the genus *Procambarus* than with those species of the other genera. The first pleopod of the male is very similar to that of the cavernicolous species inhabiting the same range, (i.e., *Procambarus pallidus*, *lucifugus lucifugus*, and *lucifugus alachua*) and to the surface species, *P. pictus* and *pubescens*.

Genus CAMBARELLUS Ortmann 1905a: 97

Type, designated by Ortmann 1905a: 106, *Cambarus montezumae* Saussure.

*Diagnosis*.—First pleopod of first form male terminating in three distinct parts; the cephalic process is always absent; the three terminals may be spiniform, somewhat truncate, spatulate or even trough-like. In the male hooks are present on the ischiopodites of the second and third pereopods. This genus includes a group of very small crayfish; specimens seldom reach a length of two inches. Third maxillipeds proportionally of normal size, with a row of teeth along the inner margin of the ischiopodite.

This genus includes all of the species listed by Faxon (1914) as belonging to his group V.

Genus ORCONNECTES Cope 1872: 419

Type, by monotypy, *Orconectes inermis* Cope.

*Diagnosis*.—First pleopod of first form male terminating in two distinct parts, both parts ending in straight or gently curved, short or long spines (occasionally the central projection, "outer part," terminates in a blade-like process). Never is a strongly developed shoulder present on the cephalic margin near the tip of the appendage. The central projection is corneous while the mesial process is usually much softer. In the male, hooks are generally

<sup>6</sup> Dr. C. J. Goodnight has kindly identified these worms for me.

present on the ischiopodite of the third pereopod only, but occasionally they are present on that of the third and fourth pereopods. Third maxillipeds of normal size with a row of teeth along the inner margin of the ischiopodite.

*Discussion.*—Cope described *Orconectes inermis* in 1872, and it was later synonymized with *Cambarus pellucidus* (Tollkampf).<sup>7</sup> In 1885 Faxon placed *Cambarus pellucidus* in his group I, because it had hooks on the ischiopodites of the third and fourth pereopods. In 1905 Ortmann placed this species in his subgenus *Faxonius*. In 1914 Faxon removed *pellucidus* from Ortmann's *Faxonius* and placed it with his group III (group II and III of Faxon = *Cambarus* of Ortmann). Since Creaser (1933) used *Faxonius* as a generic name, the relationships of *pellucidus* have become of utmost importance in determining the validity of the name *Faxonius*. I fully agree with Ortmann in the following quotation: "This subgenus [*Faxonius*] corresponds to Faxon's fourth group, with the addition of *C. pellucidus*. As regards the latter species, which Faxon places with his first group, apparently chiefly on account of the presence of hooks on the third and fourth pereopods in the male, it is easy to see that the sexual organs do not agree with the *blandingi*-type. Faxon himself says (1885, p. 42), that they are very simple, and generally admits that this species unites characters of different groups. Looking at the figures of the sexual organs given by Hagen (Ill. Cat. Mus. Harvard, 3, 1870, pl. I, f. 68-71), in Hay P.U.S. Mus., 16, 1893, pl. 45, f. 11-14), I fail to see any similarity to any of the species of the subgenus *Cambarus*, [=synonym of *Ortmannicus* Fowler], but their shape approaches rather closely that of some species of Faxon's fourth group, namely: *C. limosus*, *indianensis*, and *sloanei*. Indeed, in *C. pellucidus* this organ is different from any of these, but it agrees with them in the more or less straight and simple form, with the outer and inner parts separated at the tips for a short distance; there is also no trace of a terminal truncation. The rostrum and the chelae are rather primitive in *C. pellucidus*, while carapace and areola are peculiar, which is possibly a character due to the subterranean life (see Faxon).

"If we place *C. pellucidus* with the species of the fourth group named above, it loses its isolated position also with reference to the geographical distribution; it is found in a region (Kentucky and southern Indiana), where at least two of the above species are found: *C. indianensis* and *sloanei*.

"I think, that *C. pellucidus* is a rather primitive form, connecting the subgenus *Faxonius* with the more primitive forms of *Cambarus* (*diguetti*-group), and that the development of an additional pair of hooks on the fourth pereopods is a parallelism to the similar tendency in the more highly advanced forms of the subgenus *Cambarus* (*blandingi* group): to the latter, *C. pellucidus* has no direct relation at all." (Ortmann 1905a: 107-108.)

With the discovery of the subspecies *Cambarus pellucidus australis* Rhoades, in the Alabama caves, there can now be little doubt as to the relationship of *C. pellucidus* with the other *Cambarinae*. This new crayfish bears hooks only

<sup>7</sup> Regardless of the status of the species *inermis*, which I think is a valid species, the name *Orconectes* is still available for this group.

on the third walking legs, but in other characters is close enough to *C. pellucidus* (Tellkamp) so that Rhoades (1941: 142) considered it a subspecies. Since Faxon's only criterion for placing this species in the group that he did was, apparently, the presence of hooks on the ischiopodites of both the third and fourth pereopods, the fact that a subspecies of *pellucidus* possesses these hooks only on the third pereopod would seem to indicate that Ortmann, as quoted above, was justified in attributing the resemblance to parallelism.

Additional evidence for this assumption was indicated by Hay (1893: 285) when he pointed out that one of the specimens from Wyandotte Cave possessed hooks only on the ischiopodites of the third pereopods, whereas "the hook on the fourth pair of legs is represented by a low, almost indistinguishable tubercle."

It is further pertinent that in 1931 Creaser described *Cambarus* (*Faxonius*) *peruncus* from the Ozark Region, and writes regarding it: "*C. peruncus*, without question, is a member of the subgenus *Faxonius* as defined by Ortmann (1905, p. 97). The blind cave species, *C. pellucidus*, assigned by Ortmann (1905, p. 111) to the subgenus *Faxonius*, also has hooks on the third and fourth walking legs. Ortmann argues that this condition must have arisen independently since the other members of *Faxonius*, without exception save for the present species, have only the third pair of legs bearing hooks. Faxon (1914, p. 415) lists *C. pellucidus* under the subgenus *Cambarus*. In any event we now have evidence with the discovery of *C. peruncus* of an independent acquisition (or a primitive retention of two pairs of hooks within the subgenus *Faxonius*." (Creaser 1931: 10.)

Since Creaser made no statements concerning his use of *Faxonius* as a generic name, it is left to conjecture as to why he used *Faxonius* instead of *Orconectes*. The fact that *Orconectes inermis* (genotype of *Orconectes*) is a synonym of *Cambarus pellucidus* to some authors (to Ortmann it would now be *Faxonius pellucidus*) does not make *Orconectes* invalid if *pellucidus* is placed in a generic category other than *Cambarus*. Therefore the name *Orconectes* must be used to replace the generic name *Faxonius* as used by Creaser. Therefore all of the species of Faxon's group VI (1914), *Cambarus pellucidus*, *Cambarus clypeatus*, and the species listed below should be referred to the genus *Orconectes*.

#### ORCONECTES CREOLANUS (Creaser)

*Faxonius creolanus* Creaser, Occ. Pap. M.M.Z., 1933, No. 275, pp. 16-19, 1 pl.

*Type Locality*.—Stream tributary to the Amite River, one-half mile north of Ethel, East Feliciana Parish, Louisiana. *Holotype*, M.M.Z., No. 53332 (1♂, form I); *Allotype*, M.M.Z., No. 53333 (1♀); *Paratypes*: M.M.Z., Nos. 53334, 53335, 53336.

#### ORCONECTES IMMUNIS PEDIANUS (Creaser)

*Faxonius immunis pedianus* Creaser, Occ. Pap. M.M.Z., 1933, No. 275, pp. 14-16.

*Type Locality*.—Reservoir at Englewood, Denver County, Colorado. *Holo-*

type, M.M.Z., No. 53328 (1♂, form I); Allotype, M.M.Z., No. 53329 (1♀); Paratypes: M.M.Z., Nos. 52830, 53331, 53330, 53272.

ORCONNECTES LUTEUS (Creaser)

*Faxonius luteus* Creaser, Occ. Pap. M.M.Z., 1933, No. 275, pp. 7-10, 1 pl.

*Type Locality*.—Niangua River at mouth of Greasy Creek, 5 miles south-east of Buffalo, Dallas County, Missouri. *Holotype*, M.M.Z., No. 53305 (1♂, form I); *Allotype*, M.M.Z., No. 53306 (1♀); *Paratypes*: M.M.Z., No. 53307.

ORCONNECTES MENAE (Creaser)

*Faxonius menae* Creaser, Occ. Pap. M.M.Z., 1933, No. 275, pp. 5-7, 1 pl.

*Type Locality*.—Stream tributary to Irons Fork of Ouachita River at Mena, Polk County, Arkansas. *Holotype*, M.M.Z., No. 53301 (1♂, form I); *Allotype*, M.M.Z., No. 53302 (1♀); *Paratypes*: M.M.Z., Nos. 53303, 53304.

ORCONNECTES PELLUCIDUS AUSTRALIS (Rhoades)

*Cambarus pellucidus australis* Rhoades, Proc. U.S.N.M., 1941, 91(3129):142-145, 1 fig.

*Type Locality*.—Shelta Cavern, SE  $\frac{1}{4}$  NE  $\frac{1}{4}$  sec. 27, T. 3 S., R. 1 W., north of Huntsville, Madison County, Alabama. *Holotype*, U.S.N.M., No. 79363 (1♂, form I); *Allotype*, U.S.N.M., No. 79364 (1♀); *Paratypes*: U.S.N.M., No. 79365 (1♂, form II); Alabama Mus. Nat. Hist.; Personal Collection of Rendell Rhoades.

ORCONNECTES PERUNCUS (Creaser)

*Cambarus peruncus* Creaser, Occ. Pap. M.M.Z., 1931, No. 224, pp. 7-10, 1 pl.

*Type Locality*.—Little Creek, tributary to the St. Francis River, one mile northeast of Chloride, Iron County, Missouri. *Type*, M.M.Z., No. 53268 (1♂, form I); *Allotype*, M.M.Z., No. 53269 (1♀); *Paratypes*: M.M.Z., Nos. 53270 and 53271; others in U.S.N.M.

ORCONNECTES PUNCTIMANUS (Creaser)

*Faxonius punctimanus* Creaser, Occ. Pap. M.M.Z., 1933, No. 275, pp. 1-5, 1 pl.

*Type Locality*.—Rubidoux Creek at Waynesville, Pulaski County, Missouri. *Holotype*, M.M.Z., No. 53278 (1♂, form I); *Allotype*, M.M.Z., No. 53279 (1♀); *Paratypes*: M.M.Z., No. 53280 and in addition numerous others.

ORCONNECTES QUADRUNCUS (Creaser)

*Faxonius quadruncus* Creaser, Occ. Pap. M.M.Z., 1933, No. 275, pp. 10-12, 1 pl.

*Type Locality*.—Stout's Creek tributary to St. Francis River, between Ironton and Arcadia, Iron County, Missouri. *Holotype*, M.M.Z., No. 53324 (1♂, form I); *Allotype*, M.M.Z., No. 53325 (1♀); *Paratypes*: M.M.Z., Nos. 53326, 53327.

## Genus CAMBARUS Erichson 1846: 88

Type, designated by Faxon 1898: 644, *Astacus bartonii* Fabricius.

*Diagnosis*.—First pleopod of first form male terminating in two distinct parts; both short and usually heavy and tapering to a point. Both terminal elements are bent caudad and usually at about a 90 degree angle to the main shaft of the appendage. The central projection is corneous, and the mesial process is usually softer and sometimes bulbiform. Hooks are present on the ischiopodites of only the third pereopods of the male. Third maxillipeds of normal size with a row of teeth along the inner margin of the ischiopodite.

To this genus belong all of the species listed by Faxon (1914) as belonging to his group VII, with the exception of *Cambarus clypeatus* (which is placed in the genus *Orconectes*) and in addition the following species described since 1914.

## CAMBARUS BYERSI Hobbs

*Cambarus byersi* Hobbs, Amer. Mid. Nat., 1941, 26(1):118-121, 2 pls.

*Type Locality*.—Swamp area along Phifer Creek, 5.5 miles northwest of Pensacola, Escambia County, Florida, near U.S. Highway No. 90. *Holotype* and *Allotype*, U.S.N.M., No. 79342; *Paratypes*: M.C.Z. (1♀); M.M.Z. (1♀); Personal Collection, Univ. of Fla. (1♂, form I, 3♀, 3 immature ♂♂, 2 immature ♀♀).

## CAMBARUS CAHNI Rhoades

*Cambarus cahni* Rhoades, Proc. U.S.N.M., 1941, 91(3129):146-148, 1 fig.

*Type Locality*.—Belgreen Cave, NW  $\frac{1}{4}$  SW  $\frac{1}{4}$  sec. 12, T. 7 S., R. 13 W., Franklin County, Alabama. *Holotype*, U.S.N.M., No. 80031; *Allotype*, U.S.N.M., No. 80032; *Paratypes*: M.C.Z.; Alabama Mus. Nat. Hist.; Personal Collection of Rendell Rhoades.

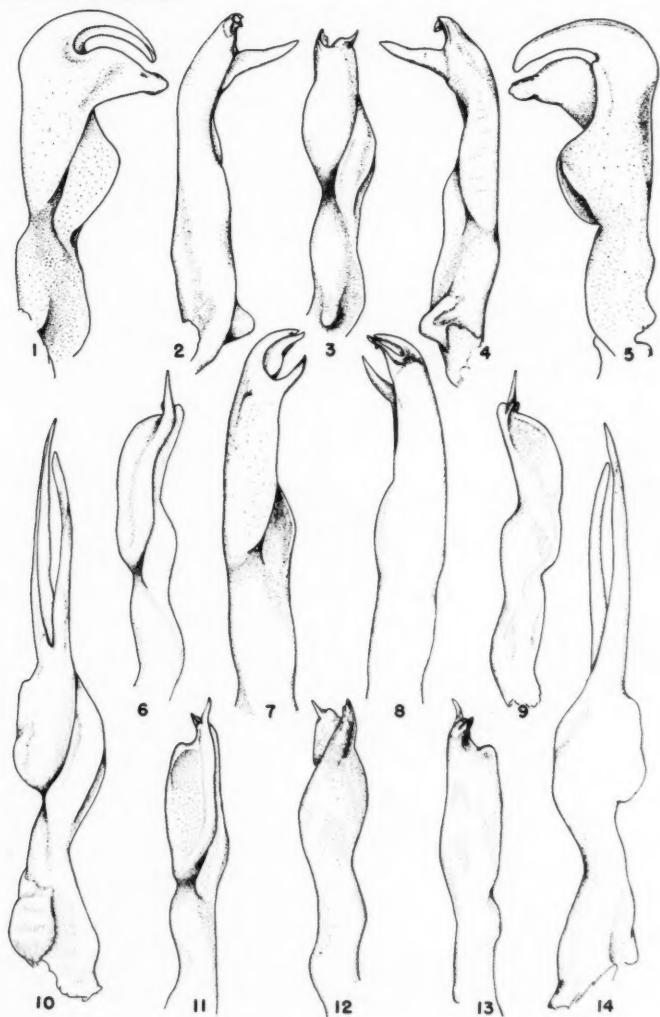
## CAMBARUS CRYPTODYTES Hobbs

*Cambarus cryptodytes* Hobbs, Amer. Mid. Nat., 1941, 26(1):110-114, 2 pls.

*Type Locality*.—2 miles south of Graceville, Jackson County, Florida, a well 60 feet deep. *Holotype*, U.S.N.M., No. 79339 (1♂, form I); *Allotype*, U.S.N.M., No. 79340 (1♀); *Paratypes*: U.S.N.M. (1♂, form II); M.C.Z. (1♀); Personal Collection, Univ. of Fla. (1♀, 1 immature ♂, 1 immature ♀).

PLATE 3.—Fig. 1. Mesial view of first pleopod of male, form I, *Cambarus floridanus* Hobbs. Fig. 2. Lateral view of first pleopod of male, form I, *Paracambarus paradoxus* (Ortmann). Fig. 3. Mesial view of first pleopod of male, form I, *Orconectes inermis* Cope. Fig. 4. Mesial view of first pleopod of male, form I, *Paracambarus paradoxus* (Ortmann). Fig. 5. Lateral view of first pleopod of male, form I, *Cambarus floridanus* Hobbs. Fig. 6. Mesial view of first pleopod of male, form I, *Procambarus barbatus* (Faxon). Fig. 7. Mesial view of first pleopod of male, form I, *Procambarus blandingii acutus* (Girard). Fig. 8. Lateral view of first pleopod of male, form I, *Procambarus blandingii acutus* (Girard). Fig. 9. Lateral view of first pleopod of male, form I, *Procambarus barbatus* (Faxon). Fig. 10. Mesial view of first pleopod of male, form I, *Orconectes rusticus rusticus* (Girard). Fig. 11. Mesial view of first pleopod of male.

form I, *Procambarus mexicanus* (Erichson). Fig. 12, Lateral view of first pleopod of male, form I, *Orconectes inermis* Cope. Fig. 13, Lateral view of first pleopod of male, form I, *Procambarus mexicanus* (Erichson). Fig. 14, Lateral view of first pleopod of male, form I, *Orconectes rusticus rusticus* (Girard). Pubescence has been removed from all structures illustrated.



## CAMBARUS FLORIDANUS Hobbs

*Cambarus floridanus* Hobbs, Amer. Mid. Nat., 1941, 26(1):114-118, 2 pls.

*Type Locality*.—"Cryptolabis Ravine," 12 miles west of Tallahassee, on St. Highway No. 19, Leon County, Florida. *Holotype* and *Allotype*, U.S.N.M., No. 79341; *Paratypes*: U.S.N.M. (1♂, form II); M.C.Z. (1♂, form I, 1♀); M.M.Z. (1♂, form II, 1♀); Personal Collection, Univ. of Fla. (1♂, form I, 4♂♂, form II, 5♀♀, 1 immature ♂, 1 immature ♀).

## CAMBARUS HUBBSI Creaser

*Cambarus hubbsi* Creaser, Occ. Pap. M.M.Z., 1931, No. 224, pp. 4-7, 2 pls.

*Type Locality*.—Little Creek, tributary to the St. Francis River, 1 mile northeast of Chloride, Iron County, Missouri. *Holotype*, M.M.Z., No. 53263 (1♂, form I); *Allotype*, M.M.Z., No. 53264 (1♀); *Paratypes*: M.M.Z., Nos. 53265, 53266, 53267; U.S.N.M.

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## The Ants of Utah<sup>1</sup>

A. C. Cole, Jr.

The state of Utah possesses a number of diversified habitats as to both topography and vegetation types. It lies entirely within the arid region of the United States, but there are high mountains separated by arid valleys and mesas. Sagebrush (*Artemisia tridentata*) ranges over a large portion of the State at the lower elevations. On the foothills of the mountain ranges is the pinyon-juniper community. Western yellow pine (*Pinus ponderosa*) dominates the plateaus. Above the yellow pine are areas of aspens, and at still higher elevations Engelmann spruce and subalpine fir abound. The alpine belt is reached at elevations of about 10,800 feet. Bordering Great Salt Lake on the west is the saltbush desert shrub region—a vegetation type which is unique in the State.

Rees and Grundmann<sup>2</sup> have published a list of 83 different ants from Utah. Five subfamilies of Formicidae containing a total of 104 different species, subspecies and varieties are now known from the State. The number of forms in each subfamily is as follows: Formicinae, 60; Myrmicinae, 34; Dolichoderinae, 8; Ponerinae, 1; and Dorylinae, 1. In the Formicinae the genus *Formica* alone accounts for 35 forms—more than twice the total number in the subfamily. Best represented in species, subspecies and varieties of Myrmicinae are the genera *Pogonomyrmex*, *Myrmica* and *Leptothorax*, whose forms number more than half the total of those in the subfamily as occurring in Utah. The dominant ants of the State are as follows: *Pogonomyrmex occidentalis*, *Formica rufa obscuripes*, *F. subpolita*, *F. fusca* var. *neorufibarbis*, *F. fusca* var. *subaenescens*, *F. fusca* var. *gelida*, *F. obtusopilosa*, *Lasius niger* var. *neoniger*, *Dorymyrmex pyramicus*, *Solenopsis molesta* var. *validiuscula* and *Monomorium minimum*.

Several forms have been described from the State. These, together with the type locality for each form, are as follows: *Pheidole pilifera artemisia* Cole (30 Mi. S. Provo), *Crematogaster coarctata* var. *mormonum* Emery (East Mill Creek Canyon in Salt Lake Co.), *Aphaenogaster uinta* Wheeler (East Mill Creek Canyon), *Pogonomyrmex occidentalis utahensis* Olsen (Zion National Park), *Myrmica sabuleti americana* Weber (Bryce Canyon), *Leptothorax nitens* Emery (American Fork Canyon in Utah Co.), *Symmyrmica chamberlini* Wheeler (near Salt Lake City), *Formica wheeleri* Creighton and *F. rufa laeviceps* Creighton (Warner Ranger Station in La Sal Mts.).

The ants range from boreal and humid elements to true desert types. In the

<sup>1</sup> Contribution no. 3, Department of Zoology and Entomology, University of Tennessee, Knoxville.

<sup>2</sup> Rees, D. M. and A. W. Grundmann, "A preliminary list of the ants of Utah," *Bull. Univ. of Utah Biol. Ser.*, VI (1940) 1-12.

sagebrush areas the dominant ants seem to be the occidental harvester (*Pogonomyrmex occidentalis*) and the thatching ant (*Formica rufa obscuripes*). Mounds of these ants are common and prominent. In the mountains, especially in cool shady canyons, nests of *Formica* spp. are abundant. At the highest elevations ants are relatively scarce, while in many of the arid valleys colonies are rather abundant and species numerous. The stone-strewn slopes of the foothills appear to be quite rich in species.

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#### KEY TO THE SUBFAMILIES OF FORMICIDAE IN UTAH<sup>3</sup>

1. Pedicel distinctly two-segmented ..... 2
- Pedicel not two-segmented ..... 3
2. Frontal carinae very closely approximated, not covering the antennal insertions ..... *Dorylinae*
- Frontal carinae covering the antennal insertions ..... *Myrmicinae*
3. Gaster constricted between its first two segments ..... *Ponerinae*
- Gaster not constricted between its first two segments ..... 4
4. Anal orifice terminal, circular and fringed with hairs ..... *Formicinae*
- Anal orifice ventral, slit-shaped and not fringed with hairs ..... *Dolichoderinae*

#### Subfamily PONERINAE

#### Genus PONERA Latreille

#### *Ponera trigona* var. *opacior* Forel

Apparently the only member of the genus known from Utah, it can be recognized by the petiole's being distinctly narrower dorsally than ventrally when viewed in profile, and by the slender graceful body. The external mandibular borders are simple. The body is 2-2.3 mm. in length, and it varies from light brown to deep black.

*Distribution*.—Springville (Grundmann).

<sup>3</sup> All keys in this paper are for the identification of the workers, unless otherwise indicated.

A single specimen was taken with workers of *Myrmica mutica* from a nest of the latter. Ordinarily these ants inhabit the soil beneath stones. Colonies are always small.

Subfamily DORYLINAE  
Genus ECITON Latreille

This genus contains the so-called "legionary ants" of the United States. Members of the genus do not construct nests of their own, but occupy temporarily those of other ants, raid the colonies and feed upon the inmates. Colonies are generally populous, and they move from place to place frequently.

*Eciton* sp.

A few small workers were collected in Milford Co. by Fautin, and were sent to Dr. Smith, of the U. S. Bureau of Entomology and Plant Quarantine, for identification. A determination to species was impossible because of the absence of the larger workers.

Subfamily MYRMICINAE

KEY TO THE GENERA OF MYRMICINAE IN UTAH

1. Postpetiole articulated to dorsal surface of gaster which is flattened dorsally, more convex ventrally and acutely pointed ..... *Crematogaster* Lund  
Postpetiole inserted at anterior end of gaster which is of the usual shape ..... 2
2. Antennae 10-segmented, with a 2-segmented club ..... *Solenopsis* Westwood  
Antennae with more than 10 segments; club, when developed, with more than 2 segments ..... 3
3. Antennae 11-segmented ..... 4  
Antennae 12-segmented ..... 6
4. Thorax and petiole without any traces of teeth or spines; pronotum never angular) ..... *Monomorium* Mayr  
Epinotum armed with spines or teeth ..... 5
5. Mesoepinotal constriction distinct ..... *Symmyrmica* Wheeler  
Mesoepinotal constriction faint or lacking ..... *Leptothorax* Mayr
6. Workers strongly dimorphic, usually without intermediates between the extreme forms; antennal club 3-segmented, longer than remainder of funiculus .....  
..... *Pheidole* Westwood  
Workers monomorphic or polymorphic, i.e., with intermediates between the major and minor forms; antennal club indistinct or shorter than remainder of funiculus ..... 7
7. Last three antennal segments, considered together, much shorter than remainder of funiculus and not forming a distinct club ..... 8  
Last three antennal segments forming a distinct club nearly as long as remainder of funiculus ..... *Leptothorax* Mayr
8. Thoracic dorsum impressed at mesoepinotal suture; (promesonotal suture usually distinct) ..... 9  
Thoracic dorsum without suture or impression ..... *Pogonomyrmex* Mayr
9. Posterior tibial spurs pectinated ..... *Myrmica* (Latreille)  
Posterior tibial spurs simple ..... 10
10. Small hypogaedic species with vestigial eyes and two keels on the clypeus .....  
..... *Stenamma* Westwood  
Medium sized species with well developed eyes and no keel on the clypeus: (thorax and legs slender) ..... *Aphaenogaster* Mayr

Genus *MONOMORIUM* Mayr  
*Monomorium minimum* (Buckley)

This small, shining, jet-black species, which is the only member of the genus known from Utah, is readily distinguishable from species in allied genera.

*Distribution*.—Clover, Little Valley Ranger Sta., Fishers Pass, Orr's Ranch—all in Tooele Co., Hooper (Knowlton); Salt Lake City (Rowe); Salt Lake Co. (Rowe, Rees); Little Willow Canyon in Salt Lake Co. (Chamberlin); Blanding (Woodbury); Swasey Springs in Millard Co. (Rees); American Fork (Rees and Moffett); 20 Mi. N. Kanab (Cole).

These ants nest beneath stones in rather moist places, or they construct small crater mounds. Some have been found nesting beneath the bark or in the wood of decaying logs.

Genus *SOLENOPSIS* Westwood

KEY TO THE SPECIES OF *SOLENOPSIS* IN UTAH

Body rather uniformly light tan or yellow, appendages lighter.....*molesta* (Say)  
Body distinctly infuscated .....*molesta* var. *validiuscula* Emery

*Solenopsis molesta* (Say)

About 1.3 mm. long, smooth and shining and with sparse and rather long hairs.

*Distribution*.—White Valley in Millard Co. (Fautin).

Apparently only this record is known from Utah. The ants nest beneath stones and logs, or under bark of decaying logs, in moist places. They have also been found occupying nest galleries of other species of ants.

*Solenopsis molesta* var. *validiuscula* Emery

Differs from the typical species chiefly in color and size (being as long as 2 mm.). It is apparently rather abundant and widely distributed in the State.

*Distribution*.—Kaysville, Logan Canyon in Cache Co., Ogden (Knowlton and Stains); Orr's Ranch, Josepa and Vernon Creek—all in Tooele Co., Current Creek in Duchesne Co., Benson in Cache Co., Moab (Knowlton); Ft. Douglass Reservation, mouth of Emigration Canyon, East Bench near Parleys Canyon, Little Willow Canyon and Lake Blanche trail—all in Salt Lake Co. (Grundmann); Salt Lake City (Rowe, Rees); La Sal Creek in La Sal Mts. in San Juan Co. (Rees); Greenriver in Emery Co. (Knowlton and F. C. Harmston); Leeds (Vasquez); Kanab, Provo (Cole).

Numerous colonies have been found nesting in the same kinds of habitats as those of the typical *molesta*.

Genus *PHEIDOLE* Westwood

Four species, subspecies and varieties are known from Utah, but none seems to be at all well represented. These ants are essentially seed-eaters, but some attend aphids, and most feed upon some dead insects. Seeds are stored in the chambers of most of the nests. There is marked dimorphism in the wingless castes. One caste, the worker, is comparatively small and has a body of rather normal proportions. The other wingless caste, the soldier, has its head much out

of proportion to the remainder of the body, the head's being large and provided with powerful mandibles. Since the workers of allied species exhibit no marked structural differences, the soldiers are necessary for a proper identification of the populations.

KEY TO THE SPECIES OF PHEIDOLE IN UTAH, FOR IDENTIFICATION OF THE SOLDIERS

1. Antennal scapes long, extending the full length of the head; legs very long and slender ..... *desertorum* Wheeler  
    Antennal scapes much shorter, not extending the full length of the head; legs not exceedingly long and slender ..... 2
2. Body length, 3.5-4 mm.; upper portion of head coarsely reticulate; a prominent connulate process near the center of the lateral surface of the postpetiole; color deep reddish brown ..... *pilifera artemisia* Cole  
    Body length, 2.3-2.5 mm.; upper portion of head not coarsely reticulate; center of the lateral surface of the postpetiole without a prominent connulate process; color reddish testaceous ..... 3
3. Head as long as broad; transverse occipital rugae rather numerous and coarse ..... *californica* Mayr  
    Head broader than long; transverse occipital rugae sparser and finer ..... *californica oregonica* Emery

*Pheidole pilifera artemisia* Cole

*Distribution*.—Springdale, Gusher (Knowlton); 30 Mi. S. Provo, type locality (Cole).

Apparently only a single colony is known from the State. It was observed by the writer on a hillslope covered with *Artemisia tridentata*. The nest was a small chamber in the soil beneath a large flat stone. The two other collections represent two stray soldiers which I have referred to this subspecies.

*Pheidole desertorum* Wheeler

*Distribution*.—Castle Cliff in Washington Co. (Knowlton).

Only a few soldiers were found, and they were strays.

*Pheidole californica* Mayr

This small ant has abundant and rather long yellowish hairs which are of uneven length on the body, suberect on the body and scapes and short and subappressed on the legs.

*Distribution*.—Ironton (Knowlton); Moab, La Sal (Knowlton and M. J. Janes); Salt Lake City (Chamberlin, Grundmann).

A few colonies were found beneath stones in rather dry grassy areas.

*Pheidole californica oregonica* Emery

*Distribution*.—Moab, Fishers Pass in Tootle Co. (Knowlton); Clover (Knowlton and M. J. Janes); Ft. Douglass Reservation in Salt Lake Co. (Grundmann); Kanab (Cole).

Nests are in the same general habitats as those of the typical *californica*. The Kanab specimens were nesting in very dry sandy soil.

Genus CREMATOGASTER Lund

Characterized chiefly by the cordate gaster which is carried somewhat curled

over the thorax when the ants are moving. Colonies are generally rather large, and nests are usually constructed beneath stones or in or under the bark of decaying logs. Many species attend aphids and coccids on plants.

KEY TO THE SPECIES OF CREMATOGASTER IN UTAH

1. Antennal scape short, scarcely surpassing the posterior border of the head; pronotum with exceedingly coarse reticulate sculpturing in addition to the very fine reticulae; (epinotal spines short, somewhat subparallel).....*vermiculata* Emery
2. Prothoracic humeri angular; sides of prothorax distinctly compressed .....*coarctata* var. *mormonum* Emery
- Prothoracic humeri rounded; sides of prothorax not distinctly compressed .....*lineolata* var. *cerasi* (Fitch)

*Crematogaster lineolata* var. (near *cerasi* Fitch)

*Distribution*.—Low, Clover, Park Valley (Knowlton); Fishers Pass in Tooele Co., Delle (Knowlton and M. J. Janes); Logan (Thatcher); Salt Lake Co. (Grundmann); Swasey Springs in Millard Co. (Rees); Provo (Cole).

Colonies are beneath logs, bark and stones.

*Crematogaster coarctata* var. *mormonum* Emery

*Distribution*.—Salt Lake City, East Mill Creek Canyon in Salt Lake Co., type locality (Chamberlin); Stansbury Island in Great Salt Lake (Titus, Grundmann).

Colonies live beneath stones and logs.

*Crematogaster vermiculata* Emery

*Distribution*.—30 Mi. S. Provo (Cole).

A single colony was found beneath a stone in a dry area of sagebrush.

Genus STENAMMA Westwood

*Stenamma brevicorne* (Mayr) var.

A single specimen of an undetermined variant of *brevicorne* was found in the State.

*Distribution*.—Logan (Thatcher).

Genus APHAENOGASTER Mayr

Members of this genus can readily be distinguished from those of *Myrmica* by their unpectinated spurs of the hind tibiae. These ants move more rapidly than those of *Myrmica*, and their colonies are generally much more populous. They nest in moist areas beneath stones and in decaying logs.

KEY TO THE SPECIES OF APHAENOGASTER IN UTAH

1. Epinotal spines prominent; antennal scapes not or but slightly surpassing the posterior corners of the head; node of petiole not conical when viewed in profile, its apex flattened, angle formed by its anterior surface and the peduncle rounded; body chestnut brown .....*subterranea occidentalis* Emery
- Epinotal spines represented by small tubercles; antennal scapes distinctly surpassing posterior corners of the head for about 1/6 their length; node of petiole conical, its apex convex, angle formed by its anterior surface and the peduncle sharp; head and thorax yellowish red, gaster dark brown or black.....*uinta* Wheeler



*Aphaenogaster subterranea occidentalis* Emery

*Distribution*.—Providence Canyon, Logan Canyon—both in Cache Co. (Knowlton and Stains); Holliday, Logan, Logan Canyon, Big Cottonwood Canyon in Salt Lake Co., Brigham (Knowlton); Univ. campus in Salt Lake City, mountain S. of Dry Canyon, Ft. Douglass Reservation, Butterfield Canyon—all in Salt Lake Co. (Grundmann); Little Willow Canyon in Salt Lake Co. (Chamberlin; Grundmann and White-lock); Salt Lake Co. (Grundmann and Rees; Gertsch); Mantua Mt. in Box Elder Co. (Knowlton and Bischoff); Thompsons (Titus?).

These well distributed ants are rather numerous in the State. Nests were found in moist areas beneath stones and in ditch banks. The colonies are moderately large.

*Aphaenogaster uinta* Wheeler

Although closely related to the preceding form, this species is very distinct from it. It has longer scapes and funicular joints, the eyes are much larger, the head is more rectangular and the epinotum lacks distinct and typical spines.

*Distribution*.—East Mill Creek Canyon in Salt Lake Co., type locality (Chamberlin); Salt Lake City, mountain S. of Dry Canyon in Salt Lake Co. (Grundmann); Point of Mountain in Salt Lake Co. (Titus); Dolphin Island in Great Salt Lake (Marshall).

Only a few nests have been found, and they were in moist soil beneath stones. The colonies are not large.

Genus *POGONOMYRMEX* Mayr

This interesting genus contains a number of forms which have been collected in Utah. All members feed upon seeds, and store them in the nests. Colonies are generally large, and both domed and crater mounds are constructed, depending upon the species concerned. The workers are monomorphic with the exception of those of *P. badius*, a species which does not occur in Utah. All species known from the State possess a more or less well developed beard of long recurved hairs on the gular region and on the lower surface of the mandibles. All species can sting, and the toxic fluid emitted by some is sufficiently potent to produce a considerable amount of pain and subsequent swelling of the lymphatics.

KEY TO THE SPECIES OF *POGONOMYRMEX* IN UTAH

1. Epinotum without distinct spines; body shining, light ferruginous red.....  
.....*californicus* (Buckley)
- Epinotum with a pair of distinct spines; head and thorax generally opaque or subopaque; color variable..... 2
2. Head distinctly concave posteriorly; densely rugose, rugae but little divergent posteriorly, interrugal spaces indistinctly or not at all sculptured; large forms..... 3
- Head not distinctly concave posteriorly, not densely rugose, rugae distinctly divergent posteriorly, interrugal spaces distinctly sculptured: small to medium sized forms..... 6
3. Head, thorax and legs deep blackish red; petiole and postpetiole brown; gaster yellowish red, often with a dark band traversing distal margin of basal segment; interrugal spaces of head and thorax finely punctate; (beard full).....  
.....*barbatus* var. *marfensis* Wheeler
- Color not as above..... 4
4. Head ferruginous red throughout; rugae of head especially and of thorax fine and rather dense.....*barbatus* var. *molefaciens* (Buckley)

- Color and sculpture different ..... 5
5. Head and thorax brownish red, gaster in part or entirely brown; cephalic rugae coarser than in *molefaciens*, interrugal spaces with delicate punctures ..... *barbatus* var. *fuscatus* Emery
- Color from ferruginous to black; head and thorax very coarsely rugose, interrugal spaces of head with traces of 2-3 fine rugules, node of petiole rather coarsely and irregularly rugose ..... *barbatus* *rugosus* Emery
6. Epinotal spines at least  $1\frac{1}{2}$  times as long as their interbasal distance; node of petiole as broad as long, or nearly so; body opaque ..... *occidentalis* (Cresson)
- Epinotal spines shorter than their interbasal distance; node of petiole distinctly longer than broad; body subopaque ..... *occidentalis* *utahensis* Olsen

*Pogonomyrmex occidentalis* (Cresson)

This is by far the most widely distributed species of the entire genus. It can be readily separated from all other members of the genus in Utah, with the exception of its subspecies *utahensis*, by the rather densely rugose head, the interrugal spaces of which are distinctly punctate; by the presence of a pair of epinotal spines; and by its ferruginous color.

*Distribution*.—Brigham, Promontory Point, Iosepa, Elberta, La Sal, Westville, Mt. Sterling in Cache Co., Blue Bench and Current Creek—both in Duchesne Co., Farmington, Little Mountain west of Ogden, Little Valley in Tooele Co., Mendon, Ouray, Big Cottonwood Canyon in Salt Lake Co., Hardup, Low, Locomotive Springs and Promontory Ridge—both in Box Elder Co., Blue Creek, Lucin, Meadow, Wild Cat Canyon in Beaver Co., Bovine, Howell, Elsinore, Salt Lake City, Virgin, Orr's Ranch in Tooele Co., Springdale, Brigham, Fillmore (Knowlton); Blue Creek (Knowlton and Fronk); Willard, Howell (Knowlton and Stains); Riverdale, Santaquin (Knowlton and Smith); Granite in Salt Lake Co. (Knowlton and Allen); Greenriver (Knowlton and F. C. Harmston); Cove in Cache Co. (Knowlton and Hardy); Logan (Knowlton and R. L. Janes); Meacham; Tintic (H. R. Harmston); Thompsons, Point of Mountain, Stansbury Island in Great Salt Lake, Mt. Pleasant, Cache Jc. (Titus); Ft. Douglass Reservation in Salt Lake Co. (Grundmann); Salt Lake Co., Summit Co. (Grundmann and Rees); Lehi (Hooker); Bluff (Stafford); Sandy, Kaysville (Klamback); Ft. Duchesne (R. L. Janes); Grantsville (Shannon); Beaver (Rowe); Brigham (Olsen); Millard Co., La Sal, La Sal Jc., Wales, Brush Creek, St. George (Rees); Leeds (Vasquez); Providence (R. L. Janes); Hardup (Thomas); Salt Lake Co. (Chamberlin); Snowville, Delle, Brigham, Ogden, Tooele, Zion Natl. Park, Kanab (Cole); Elsinore, Collinston (collectors unknown).

This is undoubtedly the most prevalent mound-building ant of the sagebrush plains. The cone-shaped pebble mounds, which are scattered about in the open areas, are frequently several feet in diameter and a foot or so in height. Surrounding each mound is a denuded area which results after the workers have cleared away the plants that grow there. The mound contains chambers in which seeds are stored and into which the brood is placed by the workers during periods of optimum mound temperatures. The nests, which continue underground, may contain thousands of individuals. The winged castes appear usually during July. At high elevations colonies are generally scarce or absent.

*Pogonomyrmex occidentalis utahensis* Olsen

I prefer to regard these ants as representing a subspecies rather than a variety of *occidentalis*. In both structure and habitat the requirements of the subspecific category are met.

It differs from the typical species by its shorter epinotal spines and its petiolar node which is distinctly longer than broad. The body surface is somewhat more shining than that of the typical *occidentalis*, and the interrugal punctures of the head and thorax are less pronounced.

*Distribution*.—Zion Natl. Park, type locality (Creighton, Cole); Kanab, St. George (Rees).

The ants were found inhabiting rather small pebble mounds in dry canyons.

*Pogonomyrmex barbatus rugosus* Emery

*Distribution*.—Greenriver (Knowlton and F. C. Hamstén); Hurricane (Grundmann); St. George (Rees); Thompsons (Titus?).

Apparently not well represented in the State, this subspecies constructs crater mounds of pebbles. The workers can sting severely.

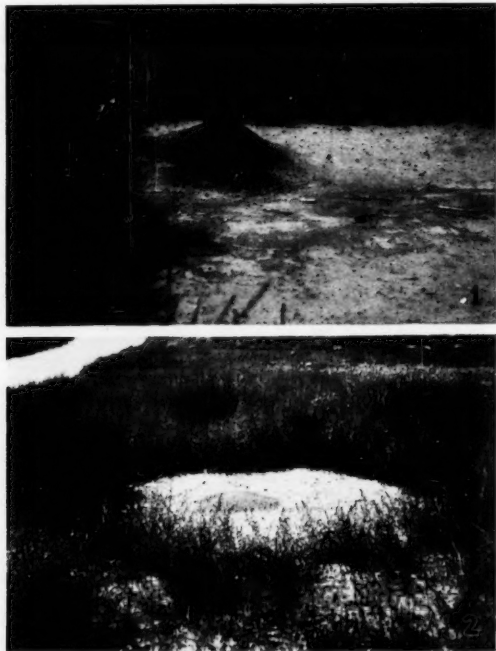


Fig. 1. Typical conical pebble mound of *Pogonomyrmex occidentalis* (Cresson) in an area of greasewood [*Sarcobatus vermiculatus* (Hook.)].

Fig. 2. Small pebble mound of *Pogonomyrmex occidentalis* (Cresson) in an area of Russian thistle (*Salsola pestifer* A. Nels.), showing the characteristic denuded area.

*Pogonomyrmex barbatus* var. *marfensis* Wheeler

Distribution.—Greenriver (Rowe).

Large crater mounds of pebbles are constructed in unshaded areas.

*Pogonomyrmex barbatus* var. *fuscatus* Emery

Distribution.—Goulding Mountain (Shaw).

Like other members of the *barbatus* group, these ants make crater mounds of pebbles.

*Pogonomyrmex barbatus* var. *molefaciens* (Buckley)

Distribution.—St. George (Tanner).

The pebble mounds frequently have rather greatly elevated craters which are more oval than spherical.

*Pogonomyrmex californicus* (Buckley)

This species lacks epinotal spines and is less robust than the forms of *barbatus*.

Distribution.—Hurricane (Rees); St. George (Tanner).

The ants frequently construct small craters of sand, but there may be nothing but an obscure hole marking the entrance to the nest in the ground. Colonies are not large.

Genus MYRMICA (Latreille)

Several forms occur in Utah. They can be distinguished readily from those of *Aphaenogaster* by the pectinate spurs on the hind tibiae. Colonies inhabit, for the most part, the soil beneath stones in moist places, or they occupy decaying logs. The workers are rather sluggish. Determination of workers to the proper subspecies and subspecies is very difficult. The following key has been adapted from one by Dr. N. A. Weber.

KEY TO THE SPECIES OF MYRMICA IN UTAH

1. Epinotal spines present ..... 2
- Epinotal spines absent ..... *mutica* Emery
2. Antennal scapes evenly bent at base and without a dorsal lamina ..... 3
- Antennal scapes with a distinctly angular bend at base and with a dorsal lamina.... 4
3. Epinotal spines long, robust, straight, blunt; head and gaster dark brown or black; thorax, petiole and postpetiole deep red to nearly black.....
- ..... *brevinodis sulcinodoides* Emery
- Epinotal spines rather slender, pointed, curved inward; color of body lighter.....
- ..... *brevinodis* Emery
4. Bend of antennal scapes with a suberect lamina at base; postpetiole with a comparatively flat ventral surface ..... *sabuleti americana* Weber
- Bend of antennal scapes otherwise ..... 5
5. Bend of antennal scapes with a high thin lamina produced anteriorly and ventrally.....
- ..... *schlenkeri emeryana* Forel
- Bend of antennal scapes otherwise ..... 6
6. Bend of antennal scapes compressed laterally ..... *scabrinodis mexicana* Wheeler
- Bend of antennal scapes compressed dorso-ventrally; (postpetiole distinctly convex ventrally) ..... *lobicornis fracticornis* Emery

*Myrmica sabuleti americana* Weber

Distribution.—Bryce Canyon, type locality (Weber).

Nests are in the soil beneath stones in moist areas.

*Myrmica brevinodis* Emery

Distribution.—Salt Lake City (Emery); Big Cottonwood Canyon in Salt Lake Co. (Grundmann).

Colonies inhabit the same type of habitat as that of the preceding ant.

*Myrmica brevinodes sulcinodoides* Emery

Distribution.—Logan, Woodland (Knowlton); Salt Lake City (Emery); River Heights in Cache Co. (Smith).

The ants nest beneath stones in moist areas.

*Myrmica lobicornis fracticornis* Emery

This appears to be the most prevalent member of the genus in Utah. Although there is a considerable variation of color among the workers, in general the thorax is reddish brown, the head considerably darker and the gaster black.

Distribution.—S. Fork of Big Cottonwood Canyon in Salt Lake Co. (Grundmann and Fox); Alta, Camas in Uinta Mts. and Soapstone Canyon in Uinta Mts.—both in Summit Co. (Grundmann); Wales, Henrys Fork Basin in Summit Co. (Rees); Salt Lake Co. (Chamberlin); Neola in Duchesne Co. (Knowlton and F. C. Harmston).

Colonies were found beneath stones and in decaying logs.

*Myrmica scheneckii emeryana* Forel

Distribution.—Leki (Hooker); Bryce Canyon (Weber).

*Myrmica scabrinodis mexicana* Wheeler

Distribution.—Salt Lake Co. (Chamberlin).

*Myrmica mutica* Emery

It can be distinguished readily from all other forms of *Myrmica* in Utah by its lack of epinotal spines. The workers are about 9-11 mm. in length and have quite a uniform reddish brown color, but the gaster may be paler than the rest of the body in some specimens.

Distribution.—Chester, Hyrum, Plain City, Blue Creek, Lake Point (Knowlton); Corrine (Knowlton and Smith); Tremonton (Knowlton and Rowe); Salt Lake City (Chamberlin, Grundmann, Cole); Salem, Woods Cross, Springville (Grundmann); Josepa (Knowlton and Janes); Tooele, Fayette, Ogden (Cole).

The ants nest in moist places in ditch banks and under stones. Sometimes they construct small craters.

## Genus LEPTOTHORAX Mayr

These ants are all small. The antenna of the worker bears usually a prominent 3-segmented club. The thorax is slender and does not possess a promesonotal suture. The epinotum bears a pair of teeth or spines. The petiole has a median ventral tooth, but the postpetiole is unarmed ventrally. The gaster is

broadly elliptical, compressed dorsoventrally and its basal three-fourths is formed by the first segment. The spurs of the median and hind legs are not pectinate. Species in the State are usually dark in color, being yellowish or reddish brown or black. Most of them have the head, thorax and pedicel sculptured and opaque. The gaster is always smooth and shining.

Apparently none of the species is at all common in the State. Those colonies which are present are difficult to find because of the diminutive size of the workers and the rather secluded locations of the nests. Colonies may be found in cavities in the soil beneath stones, in decaying wood and in the dry hollow stems of plants. Nests were found for the most part in rather moist areas, and they are undoubtedly very scarce on the sagebrush plains.

KEY TO THE SPECIES OF LEPTOTHORAX IN UTAH

1. Antennae 11-segmented ..... 2
- Antennae 12-segmented ..... 5
2. Thorax with a faint but distinct mesoepinotal impression ..... 3
- Thorax without a mesoepinotal impression; (upper surface of head and gaster, with exception of posterior edges of gastric segments, dark brown; thorax yellow or yellowish brown) ..... *rugatulus* Emery
3. Tibiae and antennal scapes without clavate hairs ..... 4
- Tibiae and antennal scapes with short, erect, clavate hairs; (body bright testaceous-ferruginous, gaster and middle of frons infuscated) ..... *hirticornis* Emery
4. Body dark brown, almost black ..... *acervorum canadensis* Provancher
- Body color much lighter ..... *acervorum canadensis* var. *yankee* Emery
5. Head very largely smooth and shining; epinotal spines very small, tooth-like, scarcely as long as the space between their bases; body yellow, in some specimens the vertex, antennal club and dorsum of gaster lightly infuscated ..... *nitens* Emery
- Head subopaque, with a satiny luster; epinotal spines robust, distinctly shorter than the spaces between their bases; body dark reddish brown, ventral portions of head, thorax and pedicel yellowish ..... *nevadensis* Wheeler

*Leptothorax rugatulus* Emery

*Distribution*.—Delle (Knowlton); Clover, Park Valley in Box Elder Co., Fishers Pass in Tooele Co. (Knowlton and M. J. Janes); White Valley in Millard Co. (Fautin).

Nests are found in the soil beneath stones in rather moist areas. Colonies are small.

*Leptothorax acervorum canadensis* Provancher

*Distribution*.—Salt Lake Co. (Chamberlin); S. Fork of Big Cottonwood Canyon, Little Cottonwood Canyon—both in Salt Lake Co. (Grundmann and Fox).

Colonies nest in or beneath decaying wood. Nests were found in decaying pine logs, in a conifer stump and in holes in dead conifers. Colonies are generally small, but some may consist of a hundred or more workers.

*Leptothorax acervorum canadensis* var. *yankee* Emery

Differs from the typical *canadensis* in its lighter coloration and somewhat longer epinotal spines. The sculpturing is finer and less rugose than in the typical form.

*Distribution*.—Utah, one of the type localities (Emery); Logan (Knowlton).

Apparently colonies are rare in the State. The ants nest in the same type of habitat as that of the typical *canadensis*.

*Leptothorax hirticornis* Emery

The head, thorax and pedicel are opaque and densely foveolate-punctate. The upper surface of the head is finely longitudinally rugose. The postpetiole is small, a little broader than long and almost trapezoidal. The hairs are erect, clavate, very short and cover the antennal scapes and legs as well as the body.

*Distribution*.—Salt Lake Co. (Chamberlin).

Information on the habitat of this species is unavailable.

*Leptothorax nitens* Emery

The head is mostly very smooth and shining; the thorax, petiole and postpetiole are opaque and finely and regularly foveolate-reticulate. In some specimens parts of the pro- and mesonotum are shining. The gaster is very smooth and shining.

*Distribution*.—American Fork Canyon in Utah Co., type locality (Collector?); Providence Canyon in Cache Co. (Knowlton and M. J. Janes).

Colonies nest in the soil, generally beneath stones.

*Leptothorax nevadensis* Wheeler

*Distribution*.—Blacksmith Fork Canyon in Cache Co. (Smith and Rowe).

These ants nest in the soil beneath stones.

Genus SYMMYRMICA Wheeler

This unique genus is known to contain but a single species, which has been found only in Utah.

*Symmyrmica chamberlini* Wheeler

The head, mandibles, thorax, petiole and postpetiole are opaque; the clypeus, frontal area, gaster and legs are shining. The antennae and legs are covered with coarse piligerous punctures. The antennae, legs and body, except the lower surfaces of the thorax and pedicel, are covered with suberect, coarse, abundant yellow hairs. There is no pubescence. The body is rich ferruginous red throughout. The gaster and legs are somewhat paler than the head, thorax and pedicel. The workers are about 3 mm. in body length.

*Distribution*.—near Salt Lake City, type locality (Chamberlin).

This is an inquiline species which colonizes in nests of *Myrmica mutica*. The ants are apparently very rare.

Subfamily DOLICHODERINAE

KEY TO THE GENERA OF DOLICHODERINAE IN UTAH

- |  |                         |
|--|-------------------------|
| 1. Scale of petiole well developed .....   | 2                       |
| Scale of petiole vestigial or absent ..... | <i>Tapinoma</i> Förster |
| 2. Epinotum with a conical elevation ..... | <i>Dorymyrmex</i> Mayr  |



- Epinotum without a conical elevation ..... 3  
 3. Body densely pubescent, ocelli usually present in large workers.....*Liometopum* Mayr  
 Body not conspicuously hairy or pubescent, ocelli absent.....*Iridomyrmex* Mayr

Genus LIOMETOPUM Mayr

*Liometopum apiculatum luctuosum* Wheeler

The entire surface of the body is rather smooth and shining. The upper surface bears only a few rather short erect hairs. Hairs are absent from the legs and antennal scapes. The body is very dark brown or black. In some specimens the antennae are dark red or yellowish red. The body length is 2.5-4.5 mm.

*Distribution*.—Myton (Grundmann, Gold); Moab, Hatch Wash near La Sal (Rees); Greenriver, Gunnison Butte in Sanpete Co. (Rowe).

The ants nest beneath stones, for the most part at high elevations (above 4,000 ft.). The workers attend aphids and coccids upon whose excretions they feed. Colonies may be very large, and the nest runways are frequently found beneath stones at an appreciable distance from the nest itself.

Genus DORYMYRMEX Mayr

These small ants nest in the open sandy soil and construct rather symmetrical craters. They move very swiftly.

KEY TO THE SPECIES OF DORYMYRMEX IN UTAH

1. Body light brown to dark brown .....*pyramicus* (Roger)  
 Color of body different..... 2  
 2. Head and thorax red, gaster black .....*pyramicus* var. *bicolor* Wheeler  
 Head, thorax and gaster yellow, the latter more or less infuscated especially  
 toward the apex .....*pyramicus* var. *flavus* McCook

*Dorymyrmex pyramicus* (Roger)

*Distribution*.—Gusher, Orr's Ranch in Tooele Co., Clive, Granite, Goshen, Blue Bench in Duchesne Co., Ft. Duchesne, Lapointe, Ouray Valley in Uinta Co. (Knowlton); Greenriver (Knowlton and F. C. Harmston); Orem (Knowlton and R. L. Janes); Granite (Knowlton and Allen); Lehi (Knowlton and Fronk); St. George (Knowlton and M. J. Janes, Grundmann, Rees); White Valley in Millard Co. (Fautin); Butterfield Canyon, Parleys Canyon—both in Salt Lake Co. (Grundmann); Hurricane (Rees); Kanab (Rees, Cole); Provo, Tooele (Cole).

This is a common ant in the drier sandy parts of the State. Usually the crater nests are aggregated in an area which may be rather circumscribed. The colonies frequently contain several hundreds of workers.

*Dorymyrmex pyramicus* var. *flavus* McCook

*Distribution*.—Gusher, Clive, Orem, Ft. Duchesne, Clover, Orr's Ranch in Tooele Co., Moab (Knowlton).

I have assigned to *flavus* workers collected at the localities cited. While these ants are not quite so pale as those from colonies in the southeastern United States, they are nevertheless consistently more like *flavus* than like the typical *pyramicus* in color.

*Dorymyrmex pyramicus* var. *bicolor* Wheeler

*Distribution*.—Moab (Knowlton and M. J. Janes); 30 Mi. S. Provo, Kanab (Cole).

Colonies seem to be uncommon in Utah although they abound in the true southwestern deserts. The small crater nests are in areas of nearly pure sand and are apparently not in those which are colonized by the typical *pyramicus*.

Genus *TAPINOMA* Förster*Tapinoma sessile* (Say)

This is a small dark brown or black ant. The petiolar scale is apparently absent.

*Distribution*.—Farmington, Logan Canyon near Logan, Cowley Canyon in Cache Co., Draper (Knowlton); Big Cottonwood Canyon in Salt Lake Co. (Grundmann and Fox, Smith, Grundmann); White Valley in Millard Co. (Fautin); S. Fork of Raft River in Box Elder Co. (Rees); Leeds (Vasquez); Logan (Stanford); Kanab (Cole).

The ants nest in the soil beneath stones in rather moist areas, in decaying logs and under bark of logs.

Genus *IRIDOMYRMEX* Mayr

Members of this genus colonize the drier areas and construct their nests in sandy soil. The nests, which are generally marked by small craters, are frequently aggregated. Some colonies are beneath stones. The workers are small and very active, and they are often rather difficult to collect.

KEY TO THE SPECIES OF *IRIDOMYRMEX* IN UTAH

1. Body rather uniformly brown or blackish; (covered with a dense pubescence which gives a pruinose effect) ..... *pruinus* (Roger)
- Body not uniformly brown or blackish ..... 2
2. Head and thorax brown, gaster paler, giving the body a bicolored appearance ..... *pruinose* var. *analis* André
- Body testaceous, vertex of head darker, tip of gaster infuscated, legs and base of gaster yellow to testaceous ..... *pruinus* var. *testaceus* Cole

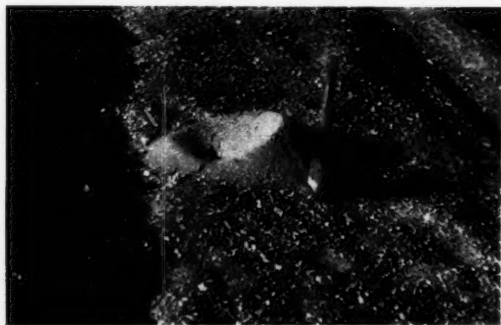


Fig. 3. Crater mound of *Dorymyrmex pyramicus* var. *bicolor* Wheeler.

*Iridomyrmex pruinosus* (Roger)

The body is smooth and about 3 mm. in length. Hairs are very sparse.

*Distribution*.—Gusher, Lucin (Knowlton); Logan Canyon in Cache Co. (Knowlton and Stains); Hurricane, mountain S. of Dry Canyon, East Bench near Parleys Canyon, Ft. Douglass Reservation—all in Salt Lake Co. (Grundmann); Johns Canyon in San Juan Co. (Rees).

A number of crater nests was found in sandy soil, and one colony nested beneath a stone.

*Iridomyrmex pruinosus* var. *analis* André

*Distribution*.—Bovine, Willow Springs, Lucin, Clover, La Sal, Big Cottonwood Canyon in Salt Lake Co., Gusher, Roosevelt (Knowlton); Moab, Clover (Knowlton and M. J. Janes); Pelican Point in Utah Co., East Bench of Parleys Canyon in Salt Lake Co. (Grundmann); Kanab, Zion Natl. Park (Cole).

The habitat and nests of this variety are like those of the typical *pruinosis*. Both forms are frequently found in the same area.

*Iridomyrmex pruinosus* var. *testaceus* Cole

*Distribution*.—Clover, Park Valley, Gusher, Lucin, Deseret, Josepa, Valley Junction (Knowlton and M. J. Janes).

The habitat and nests are similar to those of the two preceding two forms.

Subfamily FORMICINAE

KEY TO THE GENERA OF FORMICINAE IN UTAH

1. Workers polymorphic ..... *Camponotus* Mayr  
Workers not polymorphic, but often of variable size ..... 2
2. Funicular segments 2-5 shorter or not longer than succeeding segments; ocelli usually absent ..... 3  
Funicular segments 2-5 longer than succeeding segments; ocelli distinct ..... 4
3. Maxillary palpi 6-segmented ..... *Lasius* Fabricius, s. str.  
Maxillary palpi 3-segmented ..... *Lasius* (*Acanthomyops* Mayr)
4. Fourth segment of maxillary palpi distinctly longer than fifth ..... *Myrmecocystus* Wesmæl  
Fourth segment of maxillary palpi nearly as long as fifth ..... 5
5. Mandibles with broad, dentate masticatory borders; (prothoracic dorsum convex) ..... *Formica* Linné  
Mandibles narrow, falcate and pointed ..... *Polyergus* Latreille

Genus *LASIUS* Fabricius

The genus is well represented in Utah, not only in the number of different forms but also in the prevalence of colonies. Colonies are generally rather large, and most of the nests are in the soil beneath stones. The majority of the workers attends aphids and coccids on foliage and roots of plants.

KEY TO THE SPECIES OF *LASIUS* IN UTAH

1. Maxillary palpi 6-segmented ..... 2  
Maxillary palpi 3-segmented ..... 8
2. Last three segments of maxillary palpi elongated, of nearly equal length ..... 3  
Last three segments of maxillary palpi short, successively diminishing in length ..... 5
3. Scapes and legs without erect hairs ..... *niger* var. *americanus* Emery  
Scapes and legs with erect hairs ..... 4

4. Length about 4 mm.; pubescence very long and dense; ocelli small but distinct; head and gaster dark brown, thorax ferruginous ..... *niger* var. *sitkaënsis* Pergande  
Length about 3 mm.; pubescence shorter and less dense, especially on the gaster; ocelli apparently absent; body dark brown to black..... *niger* var. *neoniger* Emery
5. Tips of antennal scapes scarcely surpassing posterior corners of head ..... 6  
Tips of antennal scapes extending same distance beyond posterior corners of head.... 7
6. Color pale yellow, with whitish gaster ..... *flavus nearcticus* Wheeler  
Color brownish yellow throughout ..... *flavus claripennis* Wheeler
7. Color pale yellow; eyes small ..... *umbratus subumbratus* Viereck  
Color brownish yellow; eyes large ..... *umbratus mixtus* var. *aphidicola* (Walsh)
8. Petiole low, blunt above in profile ..... *latipes* (Walsh)  
Petiole higher, thin and acute above in profile ..... 9
9. Penultimate segments of distally thickened antennal funiculi somewhat broader than long; gaster with abundant long hairs..... *claviger* (Roger)  
Penultimate segments of but slightly thickened antennal funiculi not broader than long; gaster with sparse long hairs ..... *interjectus* Mayr

*Lasius niger* var. *americanus* Emery

The workers vary considerably in color, being from very light to dark brown. They average about 3 mm. in length.

*Distribution*.—Fishers Pass, Duchesne, Clover (Knowlton); Snowville (Knowlton, Cole); Logan Canyon in Cache Co. (Thatcher); Millard Co. (Rees); Salt Lake Co. (Chamberlin); Salt Lake City, Butterfield Canyon in Salt Lake Co., Alta (Grundmann); Provo, Tooele (Cole).

Colonies were found in the soil beneath stones, particularly in the more open and grassy areas. Some nests were observed at an elevation of 6,500 feet.

*Lasius niger* var. *neoniger* Emery

*Distribution*.—Logan Canyon and Cowley Canyon—both in Cache Co. (Knowlton); Blacksmith Fork Canyon in Cache Co. (Thatcher); Lake Blanche trail in Big Cottonwood Canyon, S. Fork of Big Cottonwood Canyon, N. Fork of City Creek Canyon, Lake Blanche—all in Salt Lake Co., Alta (Grundmann); American Fork Canyon in Utah Co. (Whitlock); 20 Mi. N. Kanab (Cole).

It is rather prevalent in the State at the higher elevations. Colonies were found to elevations of 10,000 ft., chiefly in forested places. The nests are usually beneath stones, but occasionally one will be found in the soil beneath a log.

*Lasius niger* var. *sitkaënsis* Pergande

*Distribution*.—Big Cottonwood Canyon in Salt Lake Co. (Smith); Holliday, Gusher, Snowville (Knowlton); Salt Lake City, Mill Creek Canyon in Salt Lake Co. (Grundmann); Utah Co. (Rowe); La Sal (Rees); Kanab, Zion Natl. Park (Cole).

Numerous colonies were found nesting in the soil beneath stones.

*Lasius flavus nearcticus* Wheeler

*Distribution*.—Butterfield Canyon in Salt Lake Co. (Grundmann); Bluff (Rowe); La Sal Mts. (Rees).

Three colonies were discovered. Two of these were apparently beneath stones, and the third was under dry sheep manure.

*Lasius flavus claripennis* Wheeler

Distribution.—Salt Lake Co. (Chamberlin).

Apparently only a single colony has been found in Utah. The ants nest beneath stones on warm stone-covered slopes.

*Lasius umbratus mixtus* var. *aphidicola* (Walsh)

Distribution.—Jordan Narrows (Roskalley); Ogden Canyon near Ogden, Henefer (Knowlton); Logan Canyon in Cache Co. (R. E. Nye and Knowlton); Little Willow Creek Canyon in Salt Lake Co. (Chamberlin).

Nests are in the soil under stones in rather cool, moist, shaded areas.

*Lasius umbratus subumbratus* Viereck

Distribution.—Salt Lake Co. (Chamberlin, Grundmann).

It nests beneath stones, but it is apparently very uncommon.

*Lasius interjectus* Mayr

Distribution.—Cedar City (Chamberlin); Big Cottonwood Canyon in Salt Lake Co. (Knowlton).

Nests are beneath stones.

*Lasius claviger* (Roger)

Distribution.—Lake Blanche in Wasatch Mts. in Salt Lake Co. (Grundmann).

Colonies were beneath stones at an elevation of 10,000 ft.

*Lasius latipes* (Walsh)

Distribution.—Current Creek and Blue Bench—both in Duchesne Co., Spring Canyon in Carbon Co. (Knowlton); Logan (Burrill); Salt Lake Co., Monticello (Chamberlin).

A few nests were found in the soil beneath stones. Numerous alate females were taken by Knowlton from the nests at Current Creek on August 16, 1935.

Genus FORMICA (Linné)

It is well represented in Utah. The colonies generally comprise large numbers of workers. The ants nest in the soil beneath stones and logs, or they construct domed mounds of earth or detritus. Some species which nest under stones and logs bank the sides of these objects lightly or densely with dried vegetable matter. A few species construct small craters of soil in grassy areas. The workers are rather large ants, and are generally black or brown with one or the other of these colors in combination with red.

KEY TO THE SPECIES OF FORMICA IN UTAH

1. First funicular segment about as long as the 2nd and 3rd segments together, the latter shorter or at least not longer than the penultimate segments; (frontal carinae short, subparallel, not diverging behind; small, mostly smooth, shining, dark-colored species) ..... 2
- First funicular segment distinctly shorter than the 2nd and 3rd segments together, the latter longer than the penultimate segments ..... 3

2. Antennal scapes with erect hairs; (body black or very dark brown, thorax sometimes reddish) ..... *neogagates lasioides* var. *vetula* Wheeler
- Antennal scapes without erect hairs ..... *neogagates* Emery
3. Anterior clypeal margin notched in the middle ..... 4
- Anterior clypeal margin entire ..... 9
4. Gaster strongly shining, with very short sparse pubescence ..... 5
- Gaster opaque or subopaque, with longer dense pubescence ..... 6
5. Erect hairs on head, thorax and gaster long and dense; clypeal notch indistinct in small workers ..... *perpilosa* Wheeler
- Erect hairs on head, thorax and gaster shorter and sparser; clypeal not distinct in small workers ..... *manni* Wheeler
6. Hairs on dorsal parts of body abundant, conspicuous, glistening white, obtuse or clavate ..... *obtusopilosa* Emery
- Hairs on dorsal parts of body sparse and more slender ..... 7
7. Hairs nearly always absent from thoracic dorsum and petiolar border ..... *sanguinea subnuda* Emery
- Hairs present though sparse on thoracic dorsum and petiolar border ..... 8
8. Posterior corners of head shining; head, thorax and appendages yellowish red, gaster brown ..... *sanguinea puberula* Emery
- Posterior corners of head opaque or subopaque; thorax, petiole, appendages and lower surface of head dull, yellowish brown, vertex and occiput piceous brown, gaster deep piceous brown ..... *wheeleri* Creighton
9. Body robust; head of largest workers not or scarcely longer than broad; funicular segments 2-3 longer and more slender than segments 6-8; petiole usually with a rather sharp superior border; (body opaque; color light or dark red, with brown or black gaster) ..... 10
- Body more slender; head of largest workers usually distinctly longer than broad; funicular segments 2-3 only slightly more slender than segments 6-8; petiole usually narrow, rather thick and with blunt superior border ..... 23
10. Female larger than largest workers, measuring 6-11 mm. .... 11
- Female not larger and sometimes even smaller than largest workers, measuring only 4-6 mm. .... *microgyna* var. *rasilis* Wheeler
11. Antennal scapes with erect hairs ..... 12
- Antennal scapes without erect hairs ..... 13
12. Head and thorax bright yellowish red, legs reddish brown ..... *oreas* Wheeler
- Red parts of body darker, legs dark brown ..... *oreas* var. *comptula* Wheeler
13. Frontal area opaque ..... *foreliana* Wheeler
- Frontal area smooth and shining ..... 14
14. Erect hairs absent from gula and upper surface of head and thorax ..... 15
- Erect hairs present on gula and upper surface of head and thorax ..... 17
15. Small forms (4-6.5 mm.) ..... *criniventris* Wheeler
- Larger forms (4-9 mm.) ..... 16
16. Gaster blackish brown ..... *comata* Wheeler
- Gaster reddish brown ..... *ciliata* Wheeler
17. Erect hairs on middle and hind tibiae confined to a double row of bristles along flexor surface ..... 18
- Erect hairs on middle and hind tibiae usually abundant and covering all surfaces, but at least there is a number of erect hairs besides the bristles on the flexor surface ..... 20
18. Gaster densely clothed with short erect hairs which form a thick investiture ..... *mucescens* Wheeler
- Erect hairs on gaster widely spaced, not forming a thick investiture ..... 19
19. Dorsum of thorax without erect hairs, or with no more than six erect hairs ..... *rufa haemorrhoidalis* Emery

- Dorsum of thorax with at least a dozen erect hairs, usually many more present; (clypeus and genae strongly shining) ..... *rufa laeviceps* Creighton
20. All sizes of workers extensively and deeply infuscated with piceous black; as a rule only heads of major workers are clear red and these may be tinged with black ..... *rufa melanotica* Emery
- Extensive infuscation, if present, confined to smallest workers, and color brownish rather than blackish; larger workers with head and thorax clear or at most bearing blotches of brownish shading ..... 21
21. Gaster densely pubescent, only posterior edges of segments shining, the rest opaque ..... 22
- Gaster with dilute pubescence, entire surface of each segment only a little less shining than its posterior edge ..... *rufa clivia* Creighton
22. Erect hairs on thorax long and rather unequal in length, cephalic hairs only a little less abundant and not much longer than those of thorax. *rufa obscuripes* Forel
- Erect hairs on thorax short and of about equal length, cephalic hairs longer and notably sparser ..... *rufa coloradensis* Wheeler
23. Thorax rather short; median segments of funiculi usually less than  $1\frac{1}{2}$  times as long as broad; scapes stout, distinctly curved at base; petiole flattened behind ..... 24
- Thorax long; median segments of funiculi more than  $1\frac{1}{2}$  times as long as broad; scapes slender, scarcely curved at base; petiole convex behind; (body opaque) ..... *moki* Wheeler
24. Gula with erect hairs ..... 25
- Gula without erect hairs ..... 28
25. Body shining; head of largest workers rectangular ..... 26
- Body opaque or subopaque; head of largest workers not rectangular ..... 27
26. Thorax brownish red or dark chestnut ..... *subpolita* Mayr
- Thorax yellow or yellowish brown; (head of largest workers with more nearly parallel sides) ..... *subpolita* var. *camponoticeps* Wheeler
27. Petiole broad, seen from behind cordate, notched in the middle ..... *cinerea* var. *altipetens* Wheeler
- Petiole narrower, with blunt margin, usually entire or obtusely angular in the middle; (body dark brownish, top of head and gaster blackish) ..... *cinerea* var. *neocinerea* Wheeler
28. Gaster opaque or subopaque, densely pubescent ..... 29
- Gaster more shining, very sparsely pubescent ..... 33
29. Thorax black or very dark brown ..... 30
- Thorax largely red ..... 32
30. Pubescence on gaster short, not silky ..... *fusca* Linné
- Pubescence on gaster longer, denser and silky ..... 31
31. Body black; pubescence not silvery ..... *fusca* var. *subsericea* Say
- Body dark brown; pubescence silvery ..... *fusca* var. *argentea* Wheeler
32. Gaster reddish brown; epinotum rounded in profile ..... *fusca* var. *neoclara* Emery
- Gaster black or blackish brown, somewhat bronzy; epinotum angular in profile ..... *rufibarbis* var. *gnava* Buckley
33. Thorax entirely black ..... *fusca* var. *subaenescens* Emery
- Thorax more or less red ..... 34
34. Thorax clear yellowish red throughout ..... *fusca* var. *neorufibarbis* Emery
- Thorax of large workers infuscated or black anteriorly ..... *fusca* var. *gelida* Wheeler

*Formica obtusopilosa* Emery

The head, thorax and antennae of the worker are red, and the gaster is black. The petiole is black but often has a reddish tinge. The grayish pubes-



cence is sparse except on the gaster where it is long and dense and conceals the shining surface.

*Distribution*.—Thompsons, Logan, Tremonton, Fielding, Bear River City, Lehi, Uinta, Garland, Fruitland, Duchesne, Lapoint (Knowlton); Salt Lake City (Knowlton, Titus); Blue Creek, Bonita (Knowlton and F. C. Harmston); Skull Valley in Tooele Co. (Knowlton and Bischoff); Hardup (Thomas); Cache Junction (Hagan); Dry Canyon in Salt Lake Co. (Thatcher); Stansbury Island in Great Salt Lake (Titus); Green Canyon in Cache Co. (Burrill); Gold Hill (Hammond); Forno Valley in Juab Co. (Fautin); edge of Great Salt Lake near Timpie (Cole); Thompsons (Titus?).

Nests are in the soil of grassy areas. Some colonies construct obscure craters, while others live beneath stones. Nests along Great Salt Lake were in the soil of a salt-grass area and did not possess craters or stone covers.

*Formica sanguinea puberula* Emery

*Distribution*.—Snowville (Knowlton); Stockton (Spalding); La Sal Mts. (Creighton); Wales (Rees); Tooele (Cole).

Nests are in the soil beneath stones.

*Formica sanguinea subnuda* Emery

The head and thorax vary from a rich red to more brownish. The gaster is black, but in some workers each segment is reddish or brownish basally.

*Distribution*.—Soapstone Canyon in Uinta Mts. in Summit Co., Horsecreek in Uinta Mts. (Grundmann); Henrys Fork Basin in Wayne Co., Palisade Park in Ashley Natl. Forest (Rees); Tooele, Grantsville (Cole).

Colonies were found in the soil beneath stones and logs.

*Formica wheeleri* Creighton

Very closely allied to *sanguinea puberula* and difficult to separate from it.

*Distribution*.—Warner Ranger Sta. in La Sal Mts., type locality, Blue Mts. (Creighton).

Nests were found beneath stones on open hillsides surrounded by extensive aspen groves.

*Formica perpilosa* Wheeler

The head and thorax are yellowish red, and the gaster is black.

*Distribution*.—Glendale, Orderville, Santa Clara (Knowlton); St. George (Knowlton and Stains); Stansbury Island in Great Salt Lake, Salt Lake City (Grundmann); Hurricane (Grundmann, Rees); Kanab (Cole).

Nests are generally in rather sandy areas. The ants usually construct obscure craters or low domes around the roots of trees and shrubs, particularly in irrigated areas and dry river beds.

*Formica manni* Wheeler

The head and thorax are a rich red, and the legs are a little paler and more yellowish. The tips of the funiculi, and sometimes the top of the head of the large workers, are lightly infuscated. The gaster is deep black.

*Distribution*.—Stansbury Island in Great Salt Lake (Knowlton); Hardup (Thomas); Willard (Knowlton and Thatcher); Lampe (Knowlton and F. C. Harmston);

Logan (Burrill); Leeds (Vasquez); Tule Springs in Millard Co. (Fautin); Jordan Narrows (Roskalley).

Colonies were found beneath stones in dry areas.

*Formica comata* Wheeler

The head and thorax are yellowish red, and the gaster is blackish brown except for a large reddish or yellowish spot at the base of the anal region. The pronotum and mesonotum each has a fuscous spot which is particularly evident in the smaller workers. The smaller workers have brown or black spots on the head and epinotum, and the coxae are more or less infuscated.

*Distribution*.—Mill Creek Canyon in Salt Lake Co. (Grundmann).

The colony cited was beneath a cluster of stones. The ants frequently nest under logs and stumps, and the nesting site is generally banked or covered with detritus.

*Formica ciliata* Mayr

The head, thorax and petiole of the largest workers are a rich yellowish red. The gaster is brown, but the dense pubescence gives it a gray appearance. The antennae are reddish yellow, and their tips are infuscated. The coxae, femora, and sometimes the tibiae, are dark brown. The smallest workers have the top of the head, the thoracic dorsum and the petiolar border infuscated. In some of the smallest workers the entire body, except the anterior portion of the head, is deeply infuscated.

*Distribution*.—between Blanding and Vedura (Woodbury).

Nests are in the soil under clusters of stones or beneath logs and stumps.

*Formica criniventris* Wheeler

The head and thorax are yellowish red, and the gaster is dark reddish brown, except for the yellow anal area and a yellowish spot at the base of the first segment. The tips of the funiculi and the median portions of the femora and tibiae are reddish or brownish. The smallest workers have the pronotum and mesonotum somewhat infuscated.

*Distribution*.—Boulton (Knowlton).

Colonies nest in the soil beneath clusters of stones which they bank with detritus.

*Formica oreas* Wheeler

The head and thorax are bright yellowish red, and the mandibles and antennal scapes are darker. The funiculi and legs are reddish brown. The gaster is black, with its anal segment, a large spot at the base of the first segment and often a spot on each of the sternites, yellow or red. Some of the smallest workers have the vertex, pronotum and mesonotum infuscated.

*Distribution*.—Logan (Knowlton, Titus); Blacksmith Fork in Cache Co. (Smith and Rowe); Box Elder Co. (Rees); Duck Creek in Cedar Mts. (Woodbury).

Colonies are founded in open sunny areas and beneath stones which the workers bank with detritus.

*Formica oreas* var. *comptula* Wheeler

The head and thorax are much darker than in the typical species, being reddish brown. The legs are dark brown or nearly black.

*Distribution*.—St. George (Knowlton); Cove (Knowlton and Stains); Cornish (Knowlton and Rowe, Smith); Wolf Creek in Summit Co. (Rees).

The habitat and nests are like those of the typical species.

*Formica foreliana* Wheeler

The head and thorax are brownish red; the frons, dorsal surface of the thorax, the petiole and the femora are infuscated; the gaster is black. The entire body is opaque.

*Distribution*.—Uinta Mts. in Summit Co. (Grundmann).

Colonies apparently nest beneath stones.

*Formica rufa clivia* Creighton

*Distribution*.—Logan (Thatcher).

Nests are begun under logs or stones in areas of sparse to moderate cover.

*Formica rufa laeviceps* Creighton

*Distribution*.—Warner Ranger Sta. in La Sal Mts., type locality (Creighton).

Nests are in the soil beneath stones and logs; a little detritus is often scattered about the covering object. Colonies are in areas of moderate to sparse cover.

*Formica rufa muscescens* Wheeler

*Distribution*.—Bryce Canyon (Creighton).

Habitat and nest are like those of the preceding subspecies.

*Formica rufa obscuripes* Forel

*Distribution*.—Holliday, Farmington, Fountain Green, Harrisville, Providence, Morgan, Ogden, Hooper, Midvale, Promontory, Bear River City, Amalga (Knowlton); Honeyville (Knowlton, Titus); Brigham, Harrisburg, Layton (Knowlton and Smith); Staterville (Knowlton and Thatcher); foot of Mt. Logan near Logan (Knowlton and R. E. Nye); Logan (Knowlton, Anthon, Cole); Trout Creek in Juab Co., Logan Canyon in Cache Co. (Thatcher); Huntsville (Knowlton and Hardy); Smithfield, Stansbury Island in Great Salt Lake (Titus); Lehi (Knowlton, Hooker); Salt Lake Valley near Murray, Parleys Canyon in Salt Lake Co. (Grundmann); Garland (Knowlton and Stains); Swasey Springs in Millard Co., Green Canyon in Daggett Co., Wales (Rees); Provo (Cole); Collinston, Bear River Canyon in Box Elder Co., Providence (collectors unknown).

The ants construct domed mounds of detritus in open areas. These thatched mounds are generally started around the base of some shrub, frequently sagebrush. Colonies are usually very populous, and the workers actively repel animals disturbing the nests. This is one of the most common ants in the State, and its colonies abound at the lower elevations.

*Formica rufa melanotica* Emery

*Distribution*.—mountains of Utah (Creighton).

Nests are reported in aspen groves. The ants build mounds of detritus in areas of moderate to dense cover. Colonies are generally populous.

*Formica rufa coloradensis* Wheeler

*Distribution*.—Hooper, Daniels Canyon in Wasatch Co. (Knowlton); Slaterville (Knowlton and Thatcher); Providence Lake in Ogden Canyon (R. E. Nye); Swasey Springs in Millard Co. (Rees); Duck Creek Ranger Sta. in Kane Co. (Creighton).

Nests are in the soil beneath logs and stumps in areas of moderate to heavy cover. There is a thatching of detritus constructed over the object covering the nest, and the mounds are frequently dome-shaped.

*Formica rufa haemorrhoidalis* Emery

*Distribution*.—Juab Co., Hyde Park (Knowlton); Kaysville (Knowlton and Smith); Bryce Canyon (Rowe).

Colonies are in the soil under logs and stones in areas of moderate to sparse cover. There is often a scattering of detritus over the nest periphery.

*Formica microgyna* var. *rasilis* Wheeler

The head, thorax and petiole are deep yellowish red, the mandibles and clypeus are somewhat darker and the ocellar region is often fuscous. In small workers the frons, vertex, thoracic dorsum and petiole are infuscated. The antennae are red, and the funiculi are more or less infuscated at their tips; the gaster is black. The entire body is opaque.

*Distribution*.—Salt Lake Co. (Chamebrlin); La Sal Mts. (Creighton).

Nests are under stones which are frequently banked with detritus.

*Formica fusca* Linné

*Distribution*.—Uinta Mts. in Summit Co. (Grundmann); Kanab Canyon, La Sal Creek in La Sal Mts. (Rees); Ferron (Rowe).

The ants nest beneath stones or logs, or they construct crude craters or small earthen mounds. Colonies are in the mountains at rather high elevations.



Fig. 4. Mound of the thatching ant (*Formica rufa obscuripes* Forel) in a sagebrush area.

*Formica fusca* var. *subsericea* Say

*Distribution*.—Clover, Current Creek, Fishers Pass, Snowville, Right Fork of Logan Canyon in Cache Co. (Knowlton); Logan Canyon (Thatcher); Salt Lake City, Ogden, Brigham, Grantsville, Tooele (Cole).

The ants nest under stones, or they may construct low flat "earthen beds" or mounds.

*Formica fusca* var. *subaenescens* Emery

*Distribution*.—Big Cottonwood Canyon in Salt Lake Co., Oak Creek in Millard Co., Clover, Richfield, Snowville (Knowlton); Green Canyon in Cache Co. (Knowlton and R. E. Nye, Thatcher); Logan (Knowlton, Thatcher, Anthon, Burrill); Diamond Canyon in Juab Co. (Knowlton and Thornley); Woodruff Park in Rich Co. (Knowlton and Smith); Mill Creek Canyon, Little Willow Canyon, S. Fork of Big Cottonwood Canyon, Parleys Canyon—all in Salt Lake Co. (Grundmann); Salt Lake Co. (Chamberlin, Rowe, Rees, Grundmann); Henry Fork Basin in Summit Co., Green Lake in Daggett Co. (Rees); 30 Mi. N. of Kanab (Cole); Providence (Hammond).

Nests are under stones in cold shady woods and forests, and they are generally found only at the higher elevations.

*Formica fusca* var. *gelida* Wheeler

The head and thorax are reddish brown, the upper half of the head is black and the thoracic dorsum is infuscated. The gaster is dark reddish brown or black.

*Distribution*.—Thatcher, Ouray, Iosepa, Orr's Ranch in Tooele Co., Riverdale, Orem, Brigham, Salina Co. Snowville, Hardup, Kaysville, Tremonton, Fishers Pass, Grantsville, Garland, Riverside, Willard, Wanship, Corinne, Lewiston, Amalga, St. Johns Sta., Cusher, Curlew, Park Valley and Promontory Ridge—both in Box Elder Co., Salina (Knowlton); Logan (Thatcher and Armstrong); Mill Creek Canyon, Little Cottonwood Canyon, Butterfield Canyon—all in Salt Lake Co. (Grundmann); Salt Lake City (Knowlton, Whitelock); Murray (Hawley).

The ants nest beneath stones or in rotting logs in woods and shady canyons.

*Formica fusca* var. *neorufibarbis* Emery

The head is black; the thorax, petiole, scapes and base of the funiculi are yellowish red, and the legs are a little paler; the gaster is dark reddish brown or black. There is a slight infuscation of the thoracic dorsum only in the smallest workers.

*Distribution*.—Roy, Sharon, Orem, Parowan, Cedar City, Holden, Summit, Leamington, Snowville, Richmond, Petersboro, Lehi, Brigham, Fielding, Collinston, Tremonton, Bear River City, Murray, Smithfield, Paradise, Hunter, Ogden, Trenton, Sardine Canyon in Cache Co., Laketown Canyon in Rich Co. (Knowlton); Amalga (Knowlton and Stains); Bear River City, Hooper (Knowlton and Smith); Newton (Knowlton and Rowe), Hobbie Creek (Knowlton and Sorenson); Salt Lake City (Knowlton, Grundmann); Hyde Park (Smith); Logan Canyon in Cache Co. (Thatcher); Wells-ville, Woods Cross, 20 Mi. E. of Camas in Uinta Mts., 3 Mi. above Suicide Rock in Parleys Canyon in Salt Lake Co., Soapstone Canyon in Uinta Mts. (Grundmann); Salt Lake Co. (Rees, Grundmann); Logan (Burrill, Meacham, Titus); Provo, Snowville (Cole); Ephraim, Parleys Canyon in Salt Lake Co. (Rees).

This common variety nests in the soil beneath stones. Colonies occur generally at lower elevations than those of *gelida*, and the nests are usually in drier areas.

*Formica fusca* var. *argentea* Wheeler

The body is dark reddish brown or brownish black, and the legs and antennae are generally light red or yellow. The dense pubescence gives the entire body a silvery luster.

*Distribution*.—Snowville, Delle (Knowlton); East Mill Creek in Little Willow Canyon in Salt Lake Co., Monticello (Chamberlin); Logan Canyon and Blacksmith Fork Canyon—both in Cache Co. (Thatcher); Salt Lake Co. (Grundmann); Box Elder Co., American, Sheep Creek in Ashley Natl. Forest in Daggett Co. (Rees).

Nests are beneath stones and logs in cold forests at the higher elevations.

*Formica fusca* var. *neoclara* Emery

The body and appendages are pale red with the vertex, funiculi and dorsum of the gaster infuscated.

*Distribution*.—Logan, Smithfield, Lewiston, Brigham, Wellsville (Knowlton); Salt Lake City (Grundmann).

The ants build "beds" of soil, with numerous entrances in crude, flat, confluent craters.

*Formica rufibarbis* var. *gnava* Buckley

The head, thorax, petiole and legs vary from light to dark brownish red or brown. The top of the head, and often also the pronotum and mesonotum, are infuscated; the tips of the funiculi are not infuscated. The head and thorax of the smaller workers are frequently dark brown.

*Distribution*.—Morgan, Ogden Canyon near Ogden (Knowlton); Lehi (Hooker).

These ants, which inhabit shady canyons, either nest in the soil beneath stones or they construct nests without craters in unprotected ground.

*Formica cinerea* var. *neocinerea* Wheeler

The body is dark brown, and the top of the head, the gaster and sometimes even the thoracic dorsum, are darker and more blackish.

*Distribution*.—17 Mi. S.W. of Jensen, Snowville (Knowlton); Wasatch (Knowlton and F. C. Harmston); Wellsville (Grundmann); Kanab (Cole).

The ants nest in rather open areas where they construct flat earthen mounds or nest beneath stones. Colonies are generally rather populous.

*Formica cinerea* var. *altipetens* Wheeler

The workers are blackish brown. The genae, anterior border of the clypeus, antennae (except the tips of the funiculi), petiole and legs are dark red or brownish red.

*Distribution*.—Warner Ranger Station in La Sal Mts. (Creighton); Henrys Fork Basin in Summit Co. (Rees).

The habits are the same as those of the preceding variety.

*Formica subpolita* Mayr

The body varies from brownish red to dark chestnut brown; the legs are paler, and the gaster and top of the head are black. The tips of the antennal

funiculi are infuscated, and sometimes the pronotum and mesonotum are also infuscated.

*Distribution*.—Orr's Ranch and Fishers Pass—both in Tooele Co., Iosepa, Trenton, Blanding, Nephi, Showell, Locomotive Springs in Box Elder Co., Rosebud, Grantsville, Kosmo, Blue Creek, Delta, Park Valley, Penrose, Bear River City (Knowlton); Diamond Canyon in Juab Co. (Knowlton and Thornley); St. George (Knowlton and Smith); Willard (Knowlton and Thatcher); West Point (Knowlton and M. J. Janes); Hurricane, Salt Lake Co. (Grundmann); Stansbury Island in Great Salt Lake (Titus); Swasey Springs in Millard Co. (Rees); Logan (Greene); Logan Canyon in Cache Co. (Thatcher); Provo, Ogden (Cole); Delta (collector unknown).

This common species nests in the soil beneath stones in grassy places. The colonies are rather small.

*Formica subpolita* var. *camponoticeps* Wheeler

*Distribution*.—Rosette, Clover, Orr's Ranch in Tooele Co., Snowville, Hardup, Kelton, Flux (Knowlton); Stansbury Island in Great Salt Lake, Ft. Douglass Reservation in Salt Lake Co. (Grundmann); Logan (Titus); Swasey Springs in Millard Co. (Rees); Moab (Chamberlin); Provo, Snowville (Cole).

The habits are like those of the typical species.

*Formica neogagates* Emery

*Distribution*.—Sevier, Lake Point (Knowlton); Logan (Knowlton, Burrill); Salt Lake City, Alta (Grundmann); Logan Canyon in Cache Co. (Thatcher); S. Fork of Cottonwood Canyon in Salt Lake Co. (Grundmann and Fox); White Valley in Millard Co., Tule Springs (Fautin); Promontory Point (Wetmore); Gunnison, Green-river (Rowe); Salt Lake City (Parks).

The small colonies nest under stones in open areas, although some construct small craters.

*Formica neogagates lasioides* var. *vetula* Wheeler

*Distribution*.—Salt Lake Co. (Grundmann); Ferron Reservoir in Emery Co. (Rees); Warner Ranger Sta. in La Sal Mts. (Creighton).

The habits are the same as those of the typical species.



Fig. 5. Portion of the sagebrush plains, the habitat of *Formica subpolita* Mayr, *F. rufa obscuripes* Forel and *Pogonomyrmex occidentalis* (Cresson).



*Formica moki* Wheeler

The body is a dusky reddish yellow; the gaster, top of the head, tips of the funiculi, apical border of the petiolar scale, the coxae and the femora are dark brown or fuscous; the pronotum and mesonotum are infuscated.

*Distribution*.—Milford (Bradley); Blanding (Woodbury); Bluff (Chamberlin); Parleys Canyon in Salt Lake Co. (Grundmann).

The ants nest in the soil under stones in dry open areas.

Genus POLYERGUS Latreille

Members of this genus are "slave-makers" and are often known as the "amazon ants." The workers pillage nests of *Formica* whose brood they seize and carry to the *Polyergus* colonies. When the raiders are attacked by the occupants of the nest they raid, they apparently pierce the heads or thoraxes of the inmates with their long, sharp, powerful mandibles.

*Polyergus rufescens breviceps* Emery

The body is subopaque, rather densely pubescent and entirely yellowish brown, except that the tip of the gaster is lightly infuscated. There is a very sudden and strong enlargement near the distal end of each antennal scape.

*Distribution*.—Green Canyon in Cache Co. (Knowlton and R. E. Nye); Salt Lake Co. (Knowlton); Logan Canyon in Cache Co. (Burrill); Logan (Burrill, Titus); Richfield (Rowe); Chester (Rees).

The ants nest beneath large stones with their slaves which are workers of *Formica fusca* var. *argentea*, *F. fusca* var. *subsericea*, *F. fusca* var. *neorufibarbis* or *F. cinerea* var. *neocinerea*. The mixed colonies are generally large.

Genus MYRMECOCYSTUS Wesmæl

All members of this genus are called "honey ants." Colonies vary considerably in size, but all are occupants of arid lands.

KEY TO THE SPECIES OF MYRMECOCYSTUS IN UTAH

1. Mandibles 9-toothed; head and thorax, and usually also the gaster, yellow ..... 2
- Mandibles 7-toothed; color always darker, head and thorax red or more or less infuscated ..... 3
2. Large forms, averaging more than 5 mm.; erect hairs on all surfaces of antennal scapes; (head, thorax and gaster yellow).....*mexicanus* var. *horti-deorum* McCook
- Small forms, averaging less than 5 mm.; erect hairs only on anterior surfaces of antennal scapes; (head narrow).....*mexicanus navajo* Wheeler
3. Workers polymorphic; erect hairs long, especially on posterior gastric segments; pubescence on gaster long and dense, completely obscuring the shining surface and gives the gaster a silky appearance .....*melliger mendax* Wheeler
- Workers monomorphic; erect hairs short over entire body; gastric pubescence very dilute or absent, so that the gaster is distinctly shining .....*melliger semirufus* Emery

*Myrmecocystus melliger mendax* Wheeler

The workers average more than 4 mm. in length, and the stature is extremely variable. The body is dull yellowish red, with the thorax infuscated and the gaster blackish with a silvery gray pubescence.

*Distribution*.—Wellsville (Grundmann); Swasey Springs in Millard Co. (Rees).  
Nests are made in the unprotected soil of dry open areas.

*Myrmecocystus melliger semirufus* Emery

The workers average less than 4 mm. in length, and the stature is more constant than that of the preceding subspecies. The entire body is shining. The head, thorax, legs and antennae are light yellowish red, the petiole is brownish and the gaster is black or piceous.

*Distribution*.—Lucin, Moab (Knowlton and M. J. Janes).

The ants construct nests with rather regular craters, about 6 inches in diameter, in sandy soil of dry open areas.

*Myrmecocystus mexicanus* var. *horti-deorum* McCook

*Distribution*.—Thompsons (Titus?); Bluff (Grundmann, Stafford, Woodbury); between Bluff and Blanding (Chamberlin); Gunnison Butte in Sanpete Co., Greenriver (Rowe).

Nests are constructed generally in the rocky soil of hills and ridges with sparse cover, and they have rather irregular craters made of large pellets of soil. The single nest entrance is spacious and irregular. Certain specialized workers, known as "repletes," occur in the nest chambers. These individuals contain "honey" which is stored in their crops. The crop becomes so greatly distended with the sweet liquid that the gaster gets very turgid and markedly larger than that of the normal worker. The honey-like material is obtained by the normal workers, during their foraging activities, from the exudations of aphids and coccids. This substances is then fed to the repletes.

There seems to be a concentration of colonies around Bluff.

*Myrmecocystus mexicanus navajo* Wheeler

The workers average much smaller in size than those of the preceding variety. The entire body is of a pale whitish yellow color, except the gaster which is more or less fuscous. The eyes are distinctly larger than those of *horti-deorum*.

*Distribution*.—White Valley in Millard Co. (Fautin).

The inconspicuous nests are constructed in warm dry soil of open country. The tiny entrance is surrounded by a scattering of small earthen pellets.

Genus CAMPONOTUS Mayr

This genus contains some of the largest known North American ants. It is well represented in Utah. The genus may be divided into those forms which nest in the soil beneath stones and logs and those which colonize chiefly dead wood or live in plant galls. The smaller species belong to the Caryae Group of which only a single member (*C. nearcticus* var. *decipiens*) is apparently known from the State.

KEY TO THE SPECIES OF CAMPONOTUS IN UTAH

1. Anterior clypeal border with a distinct but narrow notch; body 6-8 mm. in length;  
(head and thorax reddish brown, gaster black throughout) .....  
.....*nearcticus* var. *decipiens* Emery
- Anterior clypeal margin entire, or at most feebly and broadly excised in the  
middle; body 6-13 mm. in length ..... 2
2. Middle and hind tibiae with a row of graduated bristles on flexor surface ..... 3
- Middle and hind tibiae without such bristles ..... 7
3. Surface of gaster opaque ..... 4
- Surface of gaster shining ..... 5
4. Posterior corners of head with yellow spots, thorax yellowish red.....  
.....*sansabeanus* *vicinus* var. *luteangulus* Wheeler
- Posterior corners of head without yellow spots, thorax brownish red or chestnut,  
    gaster often red at base .....*sansabeanus* *vicinus* Mayr
5. Thorax red, gaster often red at base .....*sansabeanus* *vicinus* var. *nitidiventris* Emery
- Thorax brownish yellow ..... 6
6. Apical half of gaster infuscated .....*sansabeanus* (Buckley)
- Entire gaster yellow; (head black).....*sansabeanus* var. *torrefactus* Wheeler
7. Antennal scapes with short erect hairs; (body shining, black).....*laevigatus* (F. Smith)
- Antennal scapes without erect hairs ..... 8
8. Gaster opaque or subopaque ..... 9
- Gaster shining; (thorax red, head and gaster black) .....  
.....*herculeanus* *ligniperda* var. *noveboracensis* (Fitch)
9. Posterior portion of thorax red .....*herculeanus* var. *whymperi* Forel
- Entire thorax black .....*herculeanus* var. *modoc* Wheeler

*Camponotus sansabeanus* (Buckley)

*Distribution*.—Butterfield Canyon in Salt Lake Co., Parowan (Grundmann).  
Nests are beneath stones in dry woods.

*Camponotus sansabeanus vicinus* Mayr

*Distribution*.—Vernon, Chester (Knowlton); Big Cottonwood Canyon, Butterfield Canyon—both in Salt Lake Co. (Grundmann); Salt Lake City (English); White Valley in Millard Co. (Fautin); Trout Creek (Gardner); Tintic (H. R. Harmston); Cache Junction, Logan Canyon in Cache Co. (Titus); Moab (Chamberlin); American Fork (Rees and Moffett); Ferron (Rowe); Swasey Springs in Millard Co., La Sal Creek in La Sal Mts. (Rees).

The ants nest in the soil beneath large stones in rather dry open places.

*Camponotus sansabeanus vicinus* var. *nitidiventris* Emery

*Distribution*.—Willard, Granite, Gransville, Logan Canyon in Cache Co., Clover, Orr's Ranch and Willow Springs—both in Tooele Co. (Knowlton); Ogden (Knowlton, Cole); Blanding (Stafford); Trenton (Hammond); Benmore (Bischoff); Dolphin Island in Great Salt Lake (Marshall); Salt Lake City (Titus); Logan (Knowlton, Anthon, Davidson, Meacham); Roosevelt (Knowlton, Cutler); Farmington, Springville (Anthon); Jordan Narrows (Roskally); Providence Canyon in Cache Co. (Thatcher); Diamond Canyon in Juab Co. (Knowlton and Thornley).

Colonies are in the soil beneath stones in dry sunny areas at the higher elevations.

*Camponotus sansabeanus vicinus* var. *luteangulus* Wheeler

Distribution.—Moab (Stafford).

The ants nest in the soil beneath stones in rather open areas.

*Camponotus sansabeanus* var. *torrefactus* Wheeler

Distribution.—East Mill Creek Canyon in Salt Lake Co., Oris (Chamberlin); Ft. Douglass Reservation in Salt Lake Co. (Grundmann); Big Cottonwood Canyon in Salt Lake Co. (Knowlton); Salt Lake City (Rowe).

Nests are under stones in dry woods.

*Camponotus laevigatus* (F. Smith)

Distribution.—Beaver Canyon in Beaver Co. (Schaeffer); Aspen Grove (Stafford); Logan (Knowlton, Meacham); Logan Canyon in Cache Co. (Thatcher).

The colonies are very populous and nest in dry decayed logs and stumps chiefly in open woods.

*Camponotus herculeanus* var. *whymperi* Forel

Distribution.—Lake Blanche in Salt Lake Co., Horsecreek in Uinta Mts. (Grundmann); Henrys Fork in Summit Co. (Rees).

The ants nest in partially decayed logs and stumps, especially those of conifers. They are found at high elevations, those at Lake Blanche being at 10,000 ft.

*Camponotus herculeanus* var. *modoc* Wheeler

Distribution.—Little Willow Canyon in Salt Lake Co. (Chamberlin); S. Fork of Big Cottonwood Canyon in Salt Lake Co. (Grundmann and Fox); Logan (Greene); Logan Canyon in Cache Co. (R. E. Nye, Thatcher); Woodburn, Taylorsville (Knowlton); Strawberry Valley in Wasatch Co. (Anthon); Ferron Reservoir in Emery Co., Palisade Forest in Daggett Co. (Rees).

The nesting sites are like those of *whymperi*.

*Camponotus herculeanus ligniperdus* var. *noveboracensis* (Fitch)

Distribution.—Salt Lake Co. (Grundmann); Muellers Park in Davis Co. (Duncan); Roosevelt (Cutler).

Nests are in the soil beneath stones and logs in rather moist cool areas. Colonies are generally large.

*Camponotus nearcticus* var. *decipiens* Emery

Distribution.—East Mill Creek Canyon in Salt Lake Co. (Chamberlin).

The ants nest in dry dead wood, such as that of standing trees.

## Records and Descriptions of North American Plecoptera

### Part II. Notes on North American Perlodidae\*

John F. Hanson

Due to the unparalleled opportunity of having had for study numerous specimens of stoneflies from the great collections of the Museum of Comparative Zoology, Cornell University, and the United States National Museum, it has been possible to examine a large amount of material. Thus, I have studied the type specimens of all except two of our American species of *Perlodes* (as used by Needham and Claassen), *P. americana* and *P. minor*, the types of which are in Europe and unavailable under the present disturbed conditions. In addition, large series of specimens of several species being available, it has been possible to determine the constancy of various characters and thus to draw conclusions concerning their value as specific and generic characters. This in turn has led me to make certain taxonomical revisions embodied in the text of this paper.

The complex of North American species, which Needham and Claassen in 1925 placed in the single genus *Perlodes*, on the basis of several good, previously unpublished characters, must be divided into four genera. Of the sixteen species that have been described two have been synonymized by other authors. It has been found necessary here to synonymize eight more, so that only six of the original number remain. In addition, a study of the Cornell and M.C.Z. material has led to the discovery of three species new to science.

A comparison of types and other specimens with published information has led me to the conclusion that there is also considerable need for accurate redescription and refiguring of practically all of the species concerned. A similar need exists for the clarification of generic limits and characters.

In a careful study of this complex of species I have found Klapalek's original work to be the most valuable as concerns proper delimiting of genera. Klapalek (1904, 1912) created several new genera of Perlodidae, chiefly on the basis of types of genitalia. Four of these genera are directly concerned with our North American *Perlodes* complex. These are easily recognizable and are supported by good sternal thoracic characters. With but one exception, Miss Smith (1917) accurately placed our species in these four genera. However, her keys to the genera and species are hardly usable, since they are based for the most part on extremely variable venational characters. For some inexplicable reason, Needham and Claassen (1925) made the mistake of grouping

\* Contribution from the Department of Entomology, Massachusetts State College, Amherst, Massachusetts.

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this same complex of species into the single genus *Perlodes*. Actually, none of our species falls in the restricted genus *Perlodes* either on thoracic or on genitalic characters.

In my opinion, Klapalek in his use of genitalic characters for generic distinction has approached more nearly a true phylogenetic classification than has any other worker. I believe, however, that the most accurate understanding of phylogenetic relationships cannot be attained without a study of the entire anatomy of the species and genera concerned. The value of any apparently excellent generic character cannot be finally determined until all possible characters in any given group are compared with those of other related groups of species. This is true because in closely related families or even among genera the characters that are involved in evolutionary variations may be entirely different. For example, in the Perlidae, wing venation offers excellent generic characters, while thoracic sclerites and gills on the contrary are practically identical in structure in all genera of this family. In the Perlodidae the condition is exactly the opposite. Lack of realization of this fact by those attempting to separate genera of Perlodidae by wing venational characters alone has led to considerable taxonomic confusion. I think that failure to recognize fundamental characters is due usually to inadequate study of anatomy. Such fundamental characters can be recognized only through complete anatomical studies and comparisons of large series of specimens and species.

The present study, in addition to having thrown considerable light on the value of previously used characters, has brought out new generic characters. Almost every wing character that has ever been used in keying out Perlodidae breaks down even within a single species, at least among our North American species. Generic distinctions that have been based on wing characters are in fact so slight that the wings of one side of the body often run to a different genus than do the wings on the opposite side. There are, however, definite tendencies toward certain characteristics of venation (as has been shown by Klapalek, 1912), but there is always some overlapping of these characters so that their use for generic and specific distinctions is not effective. Thoracic dorsal and pleural regions offer little or nothing for indicating differences between genera. But I have found that the ventral thoracic structures exhibit some very marked characters that are of great importance, being also correlated with the genitalic features as worked out by Klapalek.

In the arrangement of genera adopted here, the principle underlying my decisions has been the current and very sound conception of a genus held by workers in numerous branches of taxonomy; namely, that a valid or strong genus should be based on a combination of two or more fundamental characters.

#### KEY TO GENERA TREATED IN THIS PAPER

1. Thorax entirely gill-less ..... 2
- Thorax with at least two pairs of gills ..... 3
2. With furcal pits relatively far apart; mesothoracic furcasternum with a Y-shaped suture with its arms terminating at the posterior angles of the furcal pits. Genitalia of male without sclerotized supraanal process or lateral stylets.....*Perlodes*

- With furcal pits closer together; the Y-shaped suture with its arms terminating at the anterior angles of the furcal pits of mesothorax. Genitalia of male with a distinct supraanal process. .... *Arcynopteryx*
3. With only two pairs of thoracic gills. No neck-like region joining mesothoracic basi- and furcasternum ..... *Protarcys*  
 With more than two pairs of thoracic gills. With a neck-like region joining mesothoracic basi- and furcasternum ..... 4
4. With three pairs of thoracic gills. With a short neck-like region joining the mesothoracic basi- and furcasternum. With the arms of the Y-shaped suture of the mesothorax terminating at the anterior angles of the furcal pits. .... *Megarcys*
- With three thoracic pairs and a cervical pair of gills. With a long neck-like region joining the mesothoracic basi- and furcasternum. With the arms of the Y-shaped suture terminating at the posterior angles of the furcal pits. .... *Perlinodes*

## PERLODES Banks, 1903

## Fig. 1

This genus is distinct from any of the known North American genera. *Dictyoptyerygella* is its closest relative within our faunal limits.

The submentum does not bear gills but it does bear a slight projection at the point where the gills are borne in other genera of Perlodidae. The thorax also is entirely gill-less in this genus. The conformation of the ventral thoracic structures is best understood by reference to Figure 1. Note that the furcasternum of the meso- and metathorax is not demarked from the basisternum by a suture. In the wings, crossveins are usually present between the radius and branches of Rs and M. Genitalia of male are without sclerotized supraanal process or lateral stylets; subanal lobes are short and approximated along the median line.

## ARCYNOPTERYX Klapalek, 1904

## Fig. 2

In the lack of thoracic gills this genus is similar to *Perlodes*, but differs from that genus in having submental gills and in sternal thoracic sclerites, particularly in the mesothoracic furcasternal plate and sutures. Both *Arcynopteryx* and *Megarcys* have a Y-shaped furcasternal suture with arms terminating at the anterior ends of the furcal pits of the mesosternum. But in *Arcynopteryx* the arms of this suture are nearly straight and the stem of the Y is much longer than the arms. Such is not the condition in *Megarcys* (see Figs. 2 and 3). Also, *Megarcys* has three pairs of thoracic gills, while, as mentioned, *Arcynopteryx* has none. In the wings, crossveins are present between the radius and branches of Rs and sometimes between branches of Rs and M as in *Perlodes*. Lateral stylets of supraanal process of male small and inconspicuous or absent. Lobes of tenth tergite best seen from above, since they lie flat over the abdomen.



## MEGARCYS Klapalek, 1912

Fig. 3

In this genus the submentum bears one pair of finger-like gills and the thorax bears three pairs, one on each segment. The prothoracic pair is situated in the membrane immediately anterior to the coxae. The meso- and metathoracic pairs are located at the anterior angles of their respective segments. The furcasternal Y-shaped suture, though in the relative position as in *Arcynopteryx*, is not so distinct and the arms are considerably longer and more curved. Apical wing venation as in *Arcynopteryx* but with a more pronounced tendency to have crossveins between branches of Rs and M. Lateral stylets of supraanal process large, flat, and conspicuous. Lobes of tenth tergite projecting upward, and thus are best seen in lateral aspect.

## PERLINODES Needham &amp; Claassen, 1925

Fig. 4

Needham and Claassen recognized the great divergence between the structure of the genitalia of *aurea* Smith from other species which they put in *Perlodes*. For this species they erected the subgenus *Perlinodes*.

*Perlinodes* must be raised to generic rank because of numerous very distinguishing characters in genitalia, gills, and sternal sclerites. The finger-like gills are more numerous and much longer than in other genera studied. They are located on the submentum and thorax as described for *Megarcys*; and in addition, there is a pair on the cervical sclerites. The basisternum of the meso- and metathorax is a markedly long and narrow transverse piece with a neck-like extension connecting it with the furcasternal plate (Fig. 4). This "neck" is especially marked in the mesothorax. The arms of the mesothoracic furcasternal Y-shaped suture join the furcasternal pits at their posterior end. Crossveins at apex of wing similar to those in *Arcynopteryx*. Lateral stylets of supraanal process of male very small and inconspicuous. Lobes of tenth tergite project upward. Seventh segment with a dorsal projection.

## PROTARCYS Klapalek, 1912

Fig. 5

Judging from Klapalek's drawings of the male genitalia and descriptions of the apical wing venation of *Protarcys*, it is quite likely but not certain that our species *bradleyi* and *tibialis* belong in that genus. It is therefore best to accept tentatively Miss Smith's placement of these two species in the genus *Protarcys* and avoid the possibility of producing further confusing synonymy. A close study of the genitalic and thoracic structures of *P. caudata*, the genotype of *Protarcys*, will eventually be necessary to determine the generic status of these species.

*Protarcys* has a pair of gills on the submentum and two pairs on the thorax. The thoracic gills are located in membrane on the anterior angles of the meso- and metathorax. The mesothoracic furcasternal Y is similar to that of *Perlinodes* but the basisternum is entirely different, having no constricted region leading to the furcasternal plate. Crossveins at apex of wing usually abundant and usually extending from costa to cubitus. Sometimes, however, where crossveins are much less numerous, the condition is identical to that typical of *Megarcsys*. Lateral stylets of supraanal process of male elongate and conspicuous. Lobes of tenth tergite lie over the abdomen so as to be usually best visible from above. Basal cercal segment very large.

#### SPECIFIC CHARACTERS OF GENERA TREATED IN THIS PAPER

The male genitalia offer the best taxonomic characters. Even very closely allied species can always be distinguished by the conformation of any one of several genitalic structures. The genital hooks (dorsal lobes of the tenth tergite), supraanal process, and lateral stylets all assume various significant shapes and sizes in different species. Female genitalia (subgenital plate) are usually sufficient for distinction of species, although they exhibit considerably more variation within a species than do the male genitalia.

The color of the various species is brownish varied with yellow. The coloration of the head exhibits interesting variations in pattern which are of considerable value for distinguishing the species. Although the extent of the yellow areas on the head varies somewhat, the general pattern of any given species seems to be sufficiently distinct and constant to permit of no confusing overlapping with but one exception. Other coloration characters are of less taxonomic value. Possibly, larger series of specimens may later show head color patterns to be more variable and thus of less value than here indicated. The pronotum in all except *Protarcys tibialis* and *bradleyi* has a broad median pale stripe. The meso- and metathorax are usually slightly darker than the rest of the body. Sometimes there occur on these segments pale mediodorsal markings but these usually appear only in old, faded alcoholic specimens and, in fresh specimens, may possibly not occur at all. However, well marked specimens of *P. tibialis* show distinct dorsal pale stripes on these two segments. The abdomen is generally nearly uniformly brown.

Wing venation is a very variable character, especially in this group, even in cases where different degrees of brachypterism contributing to atrophy and distortion of veins is not involved. Closely related species cannot possibly be differentiated on wing venational characters although some variational tendencies are exhibited.

Recognizable differences in size among the species do occur, but variations are very great and this character is thus not of significant taxonomic value.

As previously mentioned there is great need for accurate descriptions to replace older ones, which, according to modern standards, are incomplete and inaccurate. The available literature on the species concerned here is based largely on highly variable wing venational characters, inconstant body structures, as well as on erroneous observations. Thus, by the use of the keys of

Needham and Claassen and of Miss Smith it is very difficult to separate species of *Perlodes* s. l. with any degree of accuracy.

Though the following descriptions of species may appear to be very brief, they are intentionally so, since the primary purpose of this work is to present accurately the characters of greatest taxonomic value. No attempt is made therefore to describe under each species, characters which exhibit widely varying and overlapping tendencies or those which are practically identical for all species. All the drawings have been made from holotype or allotype specimens or have been carefully checked against such specimens. Since a considerable percentage of previously published distributional data is based on misidentified specimens, I am including the collection data of all the specimens over which I have worked in this study.

#### ARCYNOPTERYX AMERICANA Klapalek

##### Fig. 7

- 1912. *Arcynopteryx americana* Klapalek ♂ ♀, Collect. Zool. S. Longchamps, 4(1): 21-22, figs. of ♂ ♀ gen.
- 1917. Smith, Trans. Amer. Ent. Soc. 43:481-482, figs. of ♂ ♀ gen.
- 1925. *Perlodes* Needham & Claassen, Plecop. Amer. North of Mex., p. 61-62, figs. of ♂ ♀ gen.
- 1936. *Hydroperla parallela* Frison ♂, Ann. Ent. Soc. Amer. 29:261, figs. of ♂ gen. *New Synonymy*.
- 1937. *H. parallela* Frison ♀, Ill. Nat. Hist. Survey Bull. 21, art. 3, p. 90-91; figs. of head and pronotal patterns and ♀ gen. *New Synonymy*.
- 1938. *Perlodes* Ricker, Trans. Roy. Canad. Inst. 22:144.

The types of *Arcynopteryx americana* which are, we hope, intact in Berlin, are for obvious reasons not available for study. In Klapalek's original description of the species, neither figures nor description are adequate for absolute recognition of the species. However, it appears that it must be one or the other of two closely related species. One of these I am describing in this paper as new (*A. curvata*). The other I am accepting as *A. americana* as placed by Needham and Claassen (1925). I think this decision advisable especially since their identification is very plausible and the specimens on which it is based are available in the Cornell collection. Only a study of the types, which may never be available, could definitely solve this problem, however. In the meantime it becomes necessary to synonymize Frison's species *Hydroperla parallela* under *A. americana*. Frison figures the species very well, and there is no doubt that it is the same as that which Needham and Claassen placed as *A. americana*. In fact, Frison also registers his agreement with their placement of *A. americana* by his identification of several males and females of it in the U. S. National Museum. Why he described the same thing as a new species in a different genus is unknown. His figures (1936, 1937) are so excellent and detailed, however, that I am not including genitalic figures of this species in this paper.

Head color pattern as shown in Figure 7. All pale areas conspicuously yellow. Transverse pale M-line very conspicuous. Tentorial rugosities yellow.

Large yellow crown patch joined to extensive yellow region of the occiput. No dark brown color behind the compound eyes.

Length to tip of wings, 8 to 10 mm. in male, 16 to 20 mm. in female; length of body, 12 to 15 mm. in male, 15 to 20 mm. in female; length of fore wing, 5 to 6 mm. in male, 12 to 15 mm. in female.

*Male*: Ninth abdominal segment very slightly emarginate above and without spinulae. Tenth segment widely split above; dorsal lobes small, thumb-like, and bearing several spinulae. Supraanal process largely imbedded in membrane, and its lateral styles not visible when not extruded. When extruded, the supraanal process shows as a well sclerotized, nearly cylindrical process, membranous and somewhat bilobed at the tip. Lateral styles small but well sclerotized; the free part tapers rapidly and curves slightly inward to its sharply pointed apex. The membranous region between the lateral stylets and the base of the supraanal process is thickly beset with a mat of very fine hairs. See Frison, 1936, for accurate figures of the male of this species.

*Female*: Subgenital plate protrudes only slightly over segment nine; with a very broad apical emargination. See Frison, 1937, for figure of subgenital plate.

*Collection Data*: 1 ♂ Logan, Utah. 2 ♀ Logan, Utah, April 30, 1905. 1 ♂ Provo Canyon, Utah, April 4, 1938 (G. F. Knowlton). 1 ♀ Wyoming. 2 ♂ 3 ♀ Columbia River, Wenatchee, Wash., April 28, 1929 (M. D. Leonard). 2 ♂ High River, Alta., May 1, 1921 (O. Bryant). 1 ♂ Tenas Lake, B. C., 1904. 2 ♀ Lewis Lake, B. C., May, 1904. 1 ♀ Wellington, B. C., April 16, 1902.

#### *Arcynopteryx curvata* n. sp.

Figs. 13, 22

Head color pattern similar to that of *A. americana* but with the yellow crown patch often larger in extent and the tentorial rugosities not yellow. Also in this species the dark brown color extends behind the compound eyes.

Length to tip of wings, 15 to 17 mm. in male, 18 to 22 mm. in female; length of body, 15 to 17 mm. in male, 14 to 19 mm. in female; length of fore wing, 11 to 12 mm. in male, 14 to 17 mm. in female.

*Male*: Ninth segment of abdomen very slightly emarginate above and without spinulae. Tenth segment widely split above; dorsal lobes long, recurved, and bearing many spinulae. Supraanal process elongate, cylindrical, well sclerotized, membranous and finely setiferous at tip. Lateral stylets flat, straight or slightly curved near apex, and tapering to a sharp point; conspicuous when the supraanal process is extruded but not visible when that process is retracted within its membranous sheath. The membranous region between the lateral stylets and the base of the supraanal process is thickly beset with a mat of very fine hairs.

*Female*: Subgenital plate very similar to that of *A. americana*, but probably on the average slightly more protrusile and slightly more emarginate than in *A. americana*.

**Collection Data:** Holotype, male.—Wallace, Idaho, April 15 (Huellemann). Allotopotype, female.—May 12 (Huellemann). Paratopotypes.—1 ♂ April 15 (Huellemann). 4 ♀ April 28, May 4, 9 (Huellemann). Paratypes.—1 ♂ 1 ♀ Ore. Nat. Forest, Herman, Ore., 700 ft. alt., April 18, 1920 (A. C. Burrill). The holotype and allotype are in the M.C.Z.; paratypes are in the M. C. Z. and in my collection.

This species may be distinguished easily from *A. americana* in the male sex by the long recurved dorsal lobes, the larger lateral stylets (seen only when supraanal process is extruded), and the longer supraanal process. The subgenital plate of the female is indistinguishable from that of *A. americana* but this sex can be distinguished by color pattern difference as indicated above. It is easily conceivable, however, that further collecting in various regions will show intergradations of color pattern characters between these two species.

#### ARCYNOPTERYX MINOR Klapalek

Figs. 6, 14, 21

- 1912. *Arcynopteryx minor* Klapalek ♂ ♀, Collect. Zool. S. Longchamps, 4(1):22, no figs. (types in Europe).
- 1914. *Perlodes slossonae* Banks ♀, Proc. Ac. Nat. Sci. Phila. 66:608, fig. of ♀ gen. very inaccurate (type at M.C.Z.). *New Synonymy*.
- 1917. Smith, Trans. Amer. Ent. Soc. 43:483-484, no figs.
- 1917. *lineata* Smith ♀, *ibid.*, p. 476-477, fig. of ♀ gen. (type at Cornell). *New Synonymy*.
- 1917. *ignota* Smith ♀, *ibid.*, p. 479-480, fig. of ♀ gen. (type at Cornell, not in Philadelphia as stated in original description). *New Synonymy*.
- 1917. *inornata* Smith ♀, *ibid.*, p. 480-481, figs. of ♀ gen. and wings (type at Cornell, not in Phila. as stated in orig. desc.).
- 1925. *Perlodes* Needham & Claassen, Plecop. Amer. North of Mex., p. 65-66, no figs.
- 1925. *P. lineata* N. & C., *ibid.*, p. 60-61, fig. of ♀ gen.
- 1925. *P. ignota* N. & C., *ibid.*, p. 63-64, fig. of ♀ gen.
- 1925. *A. inornata* N. & C., *ibid.*, p. 59 (synonymized under *P. slossonae*).
- 1925. *P. slossonae* N. & C., *ibid.*, p. 59-60, fig. of ♀ gen.
- 1936. *P. margarita* Alexander ♂, Bull. Brooklyn Ent. Soc. 31:24-27, no figs. (type in the Mass. State College Collection). *New Synonymy*.
- 1938. *Perlodes* Ricker, Trans. Roy. Canad. Inst. 22:144, figs. of ♂ gen. (sketch figs. not absolutely accurate).

Three of the four species (*slossonae*, *lineata*, *ignota*) thrown into synonymy here for the first time were each described from unique female specimens. The wide differences indicated by drawings of the subgenital plate in their respective descriptions do not exist. Upon relaxing or boiling them out in potassium hydroxide they became very apparently identical. *P. margarita* Alexander was described before Ricker had studied and published figures of the types of *A. minor* in Europe. Since there were previously no recognizable descriptions of *A. minor* it is not surprising that Alexander was led to describe specimens of this interesting species from the White Mountains as new. Although Ricker's figures are inaccurate they suspiciously resemble the type male of *P. margarita*. Just as significant is the fact that *P. margarita* agrees perfectly with a male at

the M.C.Z. at Cambridge labelled "Arctic America," which specimen Banks of the M.C.Z. is convinced must have been collected with the male type of *A. minor* bearing the same data. It apparently came back to this continent from the British Museum with Hagen's collection. If that be the case, there is no doubt as to the identity of the male type of *A. minor*.

Head color pattern as shown in Figure 6. Head mostly brown; with the yellow crown spot usually broadly joined to occipital yellow area. A few pale post-ocular marmorations present on a brown background.

Length to tip of wings, 8 mm. in male, 20 mm. in female; length of body, 14 mm. in male, 15 to 16 mm. in female; length of fore wing, 4 mm. in male, 15 mm. in female.

*Male*: Ninth segment deeply emarginate above; with numerous heavy spinulae on the posterior margin. Tenth segment completely split dorsally; with posterior section modified into a pair of flat arms which face each other. The outer portion of these genital hooks or dorsal lobes is glabrous and nearly flat; with a small, flat, inconspicuous, membranous flange at the very tip of its broad apical region. Near the apex of each genital hook and projecting perpendicularly upward from its flat surface is a conspicuous compressed process bearing spinulae at its slightly enlarged tip. The supraanal process consists of a very long thin upwardly curving spine surrounded by an expansive membranous region when not extruded.

*Female*: Subgenital plate broad but narrowing considerably apically; extending across most of segment nine. Tip of subgenital plate bilobed, or frequently trilobed due to a smaller median lobe sometimes being present.

*Collection Data*: 1 ♂ Arctic America. 1 ♂ Artillery Lake, North West Territory, Canada, July 10, 1924 (R. H. Bedford). 1 ♀ Clinton Golden Lake, N.W.T., Can., Lat. 64°, August 5, 1924 (R. H. Bedford). 1 ♂ Fort Cudahy, Can., August 25, 1896 (W. O'Gilvie). 1 ♂ Ward, Colo. 1 ♀ Hermit Lake, Tuckerman's Rav., White Mts., N. H., July 20 (Sanborn). 1 ♀ Mt. Washington, W. Mts., N. H. (holotype of *P. slossonae*). 1 ♀ Hermit Lake, Tuckerman's Ravine, W. Mts., N. H. 3 ♂ Tuckerman's Ravine, W. Mts., N. H. The specimens listed above are in the M. C. Z.; those immediately below are in the Cornell Collection. 2 ♀ no collection data (holotypes of *A. ignota* and *inornata*). 1 ♀ Old Forge, N. Y., August 16, 1905 (J. G. Needham) (holotype of *A. lineata*); if not mislabelled this is a remarkably southern record for such an arctic species. 2 ♀ Nushagak River, Alaska, June 7, 1883 (P. J. Kajeonikoff). The specimens listed below are at M.S.C. 1 ♂ Tuckerman's Rav., Mt. Wash., W. Mts., N. H., alt. 4500 ft., July 3, 1933 (M. M. Alexander) (holotype of *P. margarita*). 2 ♀ Mt. Madison Springs Hut, W. Mts., N. H., July 3, 1939 (M. Smith).

### *Arcynopteryx picticeps* n. sp.

Figs. 8, 15

This species lay unidentified in the Cornell collection. Its thoracic structures indicate that it must be an *Arcynopteryx*. It differs markedly on head color pattern and subgenital plate from other species of *Arcynopteryx*, and therefore it is described here as new.

Head color pattern as shown in Figure 8. All pale areas conspicuously yellow. Crown area brown, with a longitudinal yellow mark between the ocelli. A broad transverse yellow band anterior to the ocelli. Circular post-ocular yellow area distinct from a transverse occipital yellow band and without marmorations. Tentorial rugosities yellow.

Length of female holotype; to tip of wings, 19 mm.; of body, 16 mm.; of fore wing, 15 mm.

*Female*: Subgenital plate nearly semicircular, very broad being nearly as wide as the abdomen itself, and extending nearly to the posterior margin of segment nine.

*Collection Data*: Holotype, female.—Paradise River, Rainier Nat. Park, Wash., August 30, 1928 (M. D. Leonard) (type deposited at Cornell Univ.).

### MEGARCYS SIGNATA (Hagen)

Figs. 9, 16, 23

1874. *Dictyopteryx signata* Hagen ♂ ♀, U. S. Geol. and Geogr. Survey Terr. Rept. 1873:575-576 (types at M.C.Z.).
1900. *D. irregularis* Banks ♀, Trans. Amer. Ent. Soc. 26:243, no figs. (type at M.C.Z.) (neallotype cannot be located).
1903. *Perlodes* Banks, Ent. News 14:241 (*Perlodes* n. g. = *Dictyopteryx* preoc.).
1905. *Perlodes* Jacobson & Bianchi, Prijamokroleja, etc., p. 628.
1907. *Perlodes* Banks, Canad. Ent. 39:327 (collection data under *P. signata* and *P. irregularis*).
1907. *Perlodes* Banks, Cat. Neur. Ins., p. 10 (cat. under *P. signata* and *P. irregularis*).
1912. *Megarcys* Klapalek, Collect. Zool. S. Longchamps, 4(1):12-13, good fig. of ♀ gen.
1912. *D. irregularis* Klapalek, *ibid.*, p. 12 (synonymized).
1917. *Megarcys* Smith, Trans. Amer. Ent. Soc. 43:472-475, figs. of ♂ ♀ gen. and wings and naiad.
1917. *Megarcys* Okamoto, Ent. Mag. (Japan) 3:81.
1925. *Perlodes* Needham & Claassen, Plecop. Amer. North of Mex., p. 55-56, inaccurate figs. of ♂ ♀ gen. and wings.
1925. *P. yosemite* N. & C. ♂ ♀, *ibid.*, p. 56-58, figs. of ♂ ♀ gen. *New Synonymy*.
1929. *Perlodes* Neave, Studies Biol. Stas. Canada 4:159 (collection data).

An examination of the type of *P. irregularis* shows that Klapalek was absolutely correct in declaring it to be a synonym of *M. signata*. How Needham and Claassen were misled into taking *P. irregularis* out of synonymy (1925), I do not know. What they have described as *P. irregularis* in their monograph is in this paper described as a new species (*M. subtruncata*). Since the male neallotype of *P. irregularis* cannot be located, I am not absolutely certain that that specimen is the same as the male of *M. subtruncata*, but the figures given by Needham and Claassen in their monograph indicate that this is probably the case. Their species, *P. yosemite*, on genitalic characters can obviously be nothing but a short-winged specimen of *M. signata* and is here thrown



into synonymy. The allotype female of *P. yosemite* has not been located, but Needham and Claassen's figure (1925) of the subgenital plate definitely indicates that it is *M. signata* also.

Lectotype and allotype specimens have been selected from the cotypes at the M.C.Z. as designated below under the collection data.

Head color pattern as shown in Figure 9. Pale crown spot of variable shape and size, usually distinct from the large occipital yellow area. Dark brown area covers the hind angles of the head.

Length to tip of wings, 12 to 20 mm. in male, 15 to 25 mm. in female; length of body, 13 to 17 mm. in male, 13 to 20 mm. in female; length of fore wing, 7 to 17 mm. in male, 11 to 20 mm. in female.

*Male*: Ninth abdominal segment with spinulae above, as shown in Figure 23. Dorsal lobes of tenth segment recurved forward and upward, blunt at tip, with numerous spinulae especially near the apex. A series of long hairs present on the anterior portion of segment ten. Supraanal process and lateral stylets lying in a partly membranous, partly sclerotized trough-like structure when not extruded. Sclerotized portion of supraanal process narrowing anteriorly to a knife-edge; with a long membranous, quite regular cylindrical structure protruding posteriorly from it. Lateral stylets narrowing distally; pointed and slightly hooked at apex.

*Female*: Subgenital plate divided by a deep cleft into two usually rounded lobes which often extend nearly to the margin of the tenth segment. In some specimens the lobes are considerably narrower than in the rounded type, but the cleft is always very deep.

*Collection Data*: Lectotype male and allotype female, Foothills, Colorado, 1873. Paratypes.—3 ♂ 2 ♀ Colorado Mts. and Mts. of the Pacific Slope, August 16 to Sept. 6, 1873 (Carpenter). 1 ♂ 2 ♀ Little Beaver Creek, near Celina, Ohio, July 18, 19, 1899 (Osburn). 1 ♀ Bridge Basin, Wyo. (S. Garman). 1 ♂ 1 ♀ Colorado Mts., and Mts. of the Pacific Slope, August 1873. 2 ♀ Roaring Fork, Colo. (Wheeler). 2 ♂ 3 ♀ Foothills, Colo. 1 ♀ Foothills, Colo., Sept., 1873 (Carpenter). 1 ♀ southwestern Colo., July 23, 1899. 1 ♀ Colo. 1 ♂ Georgetown, Colo. 1 ♂ Jasper, Alta., August 9 (C. T. Parsons). 1 ♀ Laggan, Alta., Aug. 23, 1902 (Osburn). 1 ♀ Glacier, B. C., August, 1902 (Osburn). 1 ♂ Thornhill Mt., alt. 5000 ft., Terrace, B. C. 1 ♀ Mt. Rainier, Wash. (type of *P. irregularis*). The specimens listed above are at the M.C.Z.; those below are at Cornell. 1 ♂ 1 ♀ Wyoming. 2 ♂ Tolland, Colo. (Dodds). 1 ♂ Custer Co., Colo. T. D. A. Cockerell). 3 ♀ Lawn Lake, Estes Park, Colo., August 27, 1919. 1 ♀ Kenosha Pass, Colo., August (Osler). 1 ♀ Salt Lake Co., Utah, June 10, 1910. 1 ♀ Mt. Edith Cavell, Banff Nat. Park, Alta., August 14, 1928. 1 ♂ 4 ♀ Roger's Pass, B. C., August 1908 (J. C. Bradley). 1 ♂ Roger's Pass, B. C., alt. 5525 ft., August 1, 1908. 3 ♂ 2 ♀ Roger's Pass, B. C., alt. 4500 ft., July 28, 1908 (J. C. Bradley). 1 ♂ Hawser, Selkirk Mts., B. C., June 22, 1905 (J. C. Bradley). 1 ♀ Glacier, B. C. (Mrs. Schaffer). 1 ♂ Mt. Lyell, Cal., alt. 11,000 ft., August 27, 1922 (J. F. Slevin) (holotype of *P. yosemite*) (holotype male at Cornell, not at Calif. Ac. Sci. as stated in N. & C. monograph; allotype female not located). The specimens listed below are in the U.S.N.M. 1 ♂ 1 naiad Centennial, Wyo., July 1, 1936 (I. H. Blake). 1 ♀ Platte Canyon, Colo., July (Osler). 1 ♀ Kaslo, B. C., August 16 (A. N. Caudell). 1 ♀ Roger's Pass, B. C., alt. 4500 ft., August 1, 1908.

*Megarcys subtruncata* n. sp.

Figs. 17, 24

1925. *Perlodes irregularis* Needham & Claassen ♂, Plecop. Amer. North of Mex., p. 58-59, figs. of ♂ ♀ gen. (neallotype not located).  
1929. *P. irregularis* Neave, Studies Biol. Stas. Canada 4:159 (collection data).  
1934. *P. irregularis* Neave, Canad. Ent. 66:1 (collection data).

I have placed Neave's references to *P. irregularis* here because in all probability he identified his specimens with reference to Needham & Claassen's monograph in which *P. irregularis* corresponds to the new species described here.

Head color pattern similar to that of *M. signata* (Fig. 9), very variable as to extent of pale areas, especially the occipital one.

Length to tip of wings, 22 mm. in male, 13 to 21 mm. in female; length of body, 22 mm. in male, 15 to 17 mm. in female; length of fore wing 16 mm. in male, 10 to 22 mm. in female. Further collecting will undoubtedly show that the extent of brachypterism in the male may equal or surpass that of the female.

*Male*: Ninth abdominal segment with spinulae above, as shown in Figure 24. Dorsal lobes of tenth segment recurved forward and upward, pointed at tip, with numerous spinulae especially along the lower margin. A series of long hairs present on the anterior portion of segment ten. Supraanal process and lateral stylets lying in a horizontal, mostly membranous, trough like structure when not extruded. Sclerotized portion of supraanal process narrowing anteriorly to a knife-edge; with a long posterior membranous projection which tapers abruptly near its apex to a thread-like end piece. Lateral stylets narrowing only very slightly distally and with a broad, nearly truncate apex.

*Female*: Subgenital plate bilobed, divided to its base, extending less than one half the distance across segment nine.

*Collection Data*: Holotype male.—Paradise Valley, Wash., July 17, 1920 (E. C. Van Dyke). Allotopotype, female. Paratypes.—1 ♀ Jasper, Alta., August 15, 1936 (Brues). 2 ♀ Laggan, Alta., August 29, 1925 (O. Bryant). 1 ♀ Cascade, Canada, July 7, 1937 (P. Schulthess). 1 ♀ Ainsworth, B.C., July 11, 1903 (R. P. Currie). 1 ♀ Kaslo, B.C., June 2 (H. G. Dyar). 1 ♀ Paradise Valley, Mt. Rainier, Wash., August, 1921 (A. L. Melander). 1 ♀ Tower Falls, Yellowstone Nat. Park, alt. 6300 ft., June 25, 1941 (C. P. Alexander). 1 ♀ Hidden Falls, Grand Tetons, Wyo., alt. 7000 ft., July 4, 1941 (C. P. Alexander). 1 ♂ 1 ♀ Cultus Lake, B.C., May 9, 1932 (W. E. Ricker). The holotype and allotype are in the M.C.Z.; paratypes are in the M.C.Z., the U.S.N.M., and in my collection.

This species is closely related to *M. signata*, but it can be distinguished easily from it in both sexes. The most obvious difference in the male sex is that this species has no apical hook on the lateral stylets. In the female sex the lobes of the subgenital plate are much smaller than in *M. signata*.

## PERLINODES AUREA (Smith)

Figs. 10, 18, 25

1917. *Arcynopteryx aurea* Smith ♀, Trans. Amer. Ent. Soc. 43:477-478, figs. of ♀ gen. and wings (types at Cornell Univ.)
1917. *A. vagans* Smith ♂, *ibid.*, p. 478-479, figs. of ♂ gen. and wings (types at Cornell Univ.). *New Synonymy.*
1925. *Perlodes* Needham & Claassen, Plecop. Amer. North of Mex., p. 62-63, fig. of ♀ gen. (*aurea*): p. 66-67, figs. of ♂ gen. (*vagans*); subg. *Perlodes* nov.
1927. *Perlodes* Seemann, Jour. Ent. and Zool. 19:56, ♀.

Although males and females have not been collected at the same spot, there is little doubt that *A. vagans* (described from the male sex) is by page priority a synonym of *P. aurea* (described from the female sex), since they are identical on thoracic gill and sclerite structure, on head color pattern, and in distribution. All five specimens known were collected within a radius of considerably less than 300 miles and two specimens were collected only 60 miles apart.

Head color pattern as shown in Figure 10. Predominating color of head uniform brown; tentorial rugosities darker. Occiput brown at outer angles behind the compound eyes. Post-ocular region pale and without marmorations.

Length to tips of wings, 15 mm. in male, 20 mm. in female; length of body, 15 mm. in male, 17 mm. in female; length of fore wing, 15 mm. in male, 17 mm. in female.

*Male:* From the seventh abdominal segment arises dorsally a protuberance consisting of two diverging, posteriorly directed prongs. Eighth segment normal. Ninth segment greatly enlarged below into a subgenital plate which displaces the tenth segment and the genitalia dorsalward; posterior dorsal region of ninth segment membranous. Tenth segment divided into two curious bootshaped genital hooks bearing spinulae at apex. Supraanal process sclerotized; with a terminal club which bears many tiny setae; when extruded, situated at the end of a large, bulbous, membranous region. The lateral stylets of the supraanal process are reduced to tiny sclerotized projections lying in membrane at the base of the club-shaped supraanal process, with only a very small portion projecting free. Neither in the holotype nor paratype do I find the elongate spine-like stylet described and figured by Smith; nor is there any indication that breakage has occurred.

*Female:* Subgenital plate projecting most of the distance across segment nine; more than half as wide as its segment; bilobed at apex, with a deep and broad emargination between the lobes.

*Collection Data:* 2 ♂ San Diego, Cal., April 23, 1879 (holotype and paratype of *P. vagans*). 1 ♂ Nevada Co., Cal. (C. V. Riley) (paratype). 1 ♀ holotype, California. 1 ♀ Yosemite Valley, Cal., May 18, 1921 (E. C. VanDyke).

## PROTARCYS BRADLEYI Smith

Figs. 11, 19, 26

1917. *Protarcys bradleyi* Smith ♂ ♀, Trans. Amer. Ent. Soc. 43:470-471, figs. of ♂ ♀ gen. and wings (types at Cornell).  
 1925. *Perlodes* Needham & Claassen, Plecop. Amer. North of Mex., p. 53-54, figs. of ♂ ♀ gen. and wings.

Head color pattern as shown in Figure 11. Crown area dark brown; yellow of occipital region sometimes extends slightly into the brown crown area. Ocelli lie in a pale V-shaped mark. Transverse pale M-line conspicuous but not as pale yellow as is the occipital yellow area. Post-ocular pale areas besprinkled with numerous marmorations.

Length to tip of wings, 20 mm. in male, 21 to 24 mm. in female; length of body, 20 mm. in male, 18 to 20 mm. in female; length of fore wing, 16 mm. in male, 17 to 18 mm. in female.

*Male*: Similar in general to *P. tibialis*, but the lateral stylets are flattened and taper to a sharp tip rather than being of uniform width throughout its length. Also the dorsal lobes of the tenth tergite show differences. In this species they are shorter and the posterior prominence of this segment is much broader than in *P. tibialis* (Figs. 26 and 27).

*Female*: Subgenital plate protruding over most of segment nine; evenly rounded; slightly more than half as wide as its segment.

*Collection Data*: 1 ♂ Lake Louise, Canadian Rockies, June 25, 1908 (J. C. Bradley) (holotype). 1 ♀ Roger's Pass, B.C., August 7, 1908, alt. 4500 ft. to 5000 ft. (J. C. Bradley) (allotype). 1 ♀ Ground Hog Basin, Selkirk Mts., B.C., alt. over 6000 ft., July 22 to August 7, 1905 (J. C. Bradley) (paratype). 1 ♀ Paradise Valley, Saddle Mt., Laggan, Alta., alt. 6000 to 7000 ft., August 29, 1925 (O. Bryant). The specimens listed above are in the Cornell collection; those listed below are in the M.C.Z. 1 ♂ Laggan, Alta., Canada, July 22, 1906 (Osburn). 1 ♂ Stony Lake, Granite Co., Mont., July 17, 1932 (W. L. Jellison). 1 ♂ Wallace, Idaho (Huellemann).

## PROTARCYS TIBIALIS (Banks)

Figs. 12, 20, 27

1914. *Perlodes tibialis* Banks ♂, Proc. Ac. Nat. Sci. Phila. 66:608, fig. of ♂ gen. (type at M.C.Z.).  
 1917. *dolobrata* Smith ♀, Trans. Amer. Ent. Soc. 43:469, figs. of ♀ gen. and wings. (type at Cornell, not at Phila. as stated in orig. desc.). *New Synonymy*.  
 1925. *Perlodes* Needham & Claassen, Plecop. Amer. North of Mex., p. 54-55, no figs.  
 1925. *P. dolobrata* N. & C. ♂, *ibid.*, p. 52-53, figs. of ♀ gen. and wings (neallotype ♂ at Cornell). *New Synonymy*.

Since the holotype female of *Protarcys dolobrata* is of unknown locality, there is a possibility that the subsequently described male may be a different species. But, since the two specimens agree on head color pattern, wing veins and colors, and on thoracic structures, such a possibility is very unlikely. The same similarities are held in common with the male type of *P. tibialis*, and the

genitalic features of the two males also agree. On this basis I am here synonymizing *P. dolobrata* under *P. tibialis*.

Head color pattern as shown in Figure 12. Crown area with a small pale area distinct from the transverse occipital yellow band. Transverse pale M-line conspicuous. Post-ocular pale areas with numerous conspicuous marmorations.

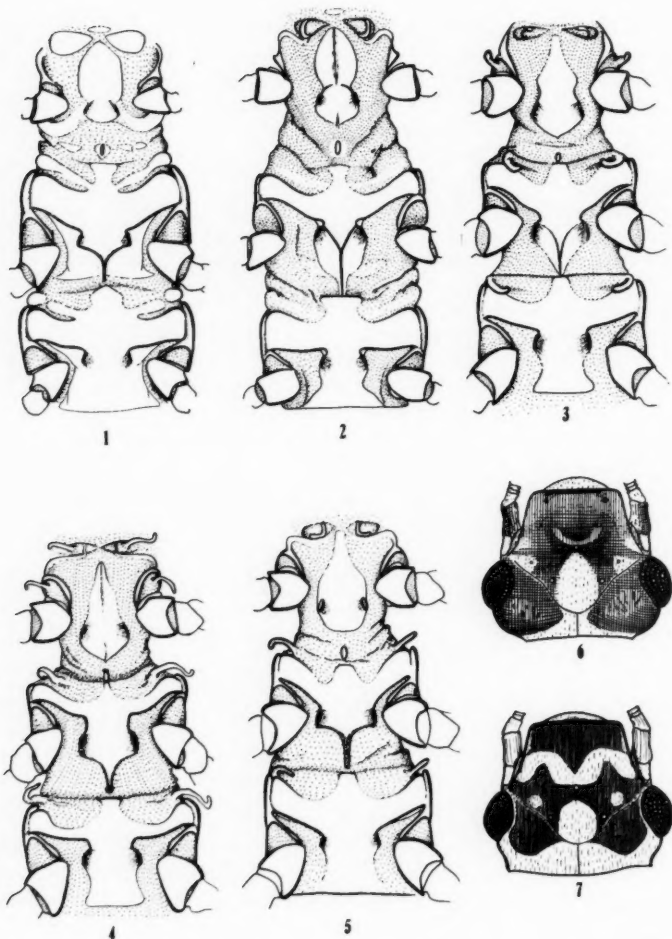
Length to tip of wings, 19 to 24 mm. in male, 23 to 29 mm. in female; length of body, 17 to 21 mm. in male, 19 to 22 mm. in female; length of fore wing, 15 to 18 mm. in male, 18 to 22 mm. in female.

*Male*: Ninth abdominal segment without spinulae above. Dorsal lobes of tenth segment slightly curved, largely membranous, quite thickly beset with setae. Supraanal process and lateral stylets lying in a mostly membranous trough when not extruded. Supraanal process elongate, mostly membranous but with a sclerotized ridge extending along the posterior median surface. Lateral stylets large and conspicuous, with flanges extending the length of the stylet so that its outer surface is concave; tip of stylet asymmetrical and usually with several sharp points. Basal segment of cerci very large.

*Female*: Subgenital plate large; protruding beyond segment nine; broadly rounded or slightly emarginate at tip; about half as wide as its segment. Subgenital plate very light brown in color, nearly white at apex; sparsely covered with minute setae.

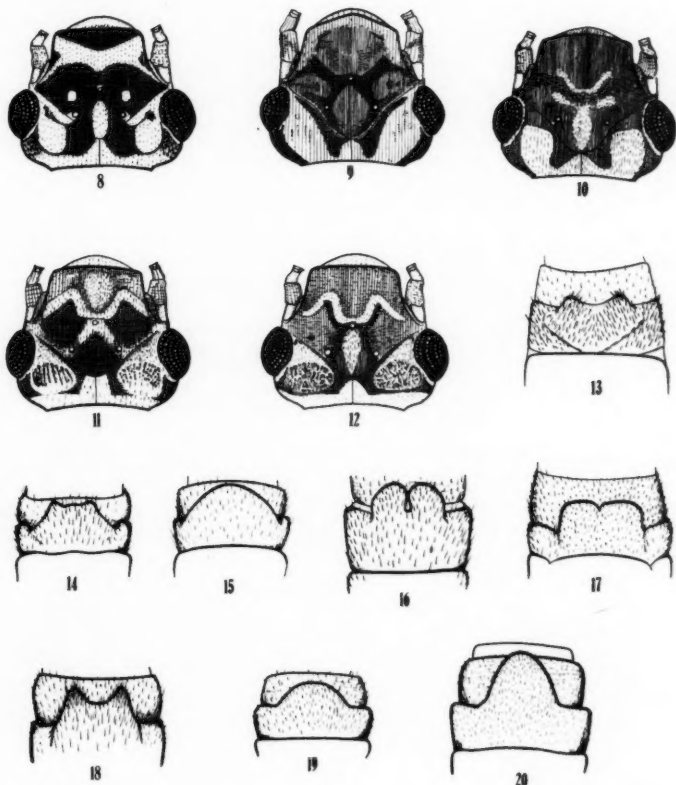
*Collection Data*: 1 ♂ Olympic Mts., Wash. (holotype). 1 ♀ no locality data (holotype of *P. dolobrata*). 1 ♂ Glacier Peak and Lake Chelan District, August, 1921 (Ruth F. Bottomley) (neallotype of *P. dolobrata*). 1 ♀ Mt. Rainier, Wash., alt. above 6000 ft., August 18, 1927. 1 ♀ Paradise Camp, Mt. Rainier, Wash., August 14, 1927 (C. R. Crosby). 1 ♀ Mt. Rainier, Wash., August 18, 1927.

From the taxonomic situation in this complex of species there is to be learned a very important lesson that merits any emphasis that it can be given. Excessive redescription of identical species under different names may be avoided in part by closer attention to at least three somewhat obvious factors. (1) Description of a new species from specimens of one sex only may be dangerous when only closely related species in the same genus are based on the other sex alone. (2) A lack of appreciation of the extent of variations of diagnostic characters in stoneflies has led to considerable synonymy. We now have large enough series of various species of stoneflies to realize that the male offers by far the most reliable specific characters in all cases. The subgenital plate of the female, which is the chief basis of species distinction in this sex in Plecoptera, varies often enough to occasion confusion of one species with another and has frequently led workers to describe extremes of variation as new species, as published synonymy shows. Many genera of stoneflies have closely related species of which the females cannot with any degree of certainty be distinguished by any known character. (3) Inexcusable carelessness of various kinds and degrees has caused much taxonomic confusion even in recent times. Use of contorted, unrelaxed, or untreated specimens has been an offender of considerable significance. Failure to examine specimens carefully for perfectly obvious characters is another; and production of radically inaccurate drawings is still another.



Ventral view of sternum of: (1) *Perlodes*, (2) *Arcynopteryx*, (3) *Megarcys*, (4) *Perlinodes*, (5) *Protarcys*. Head color pattern of: (6) *A. minor*, (7) *A. americana*.

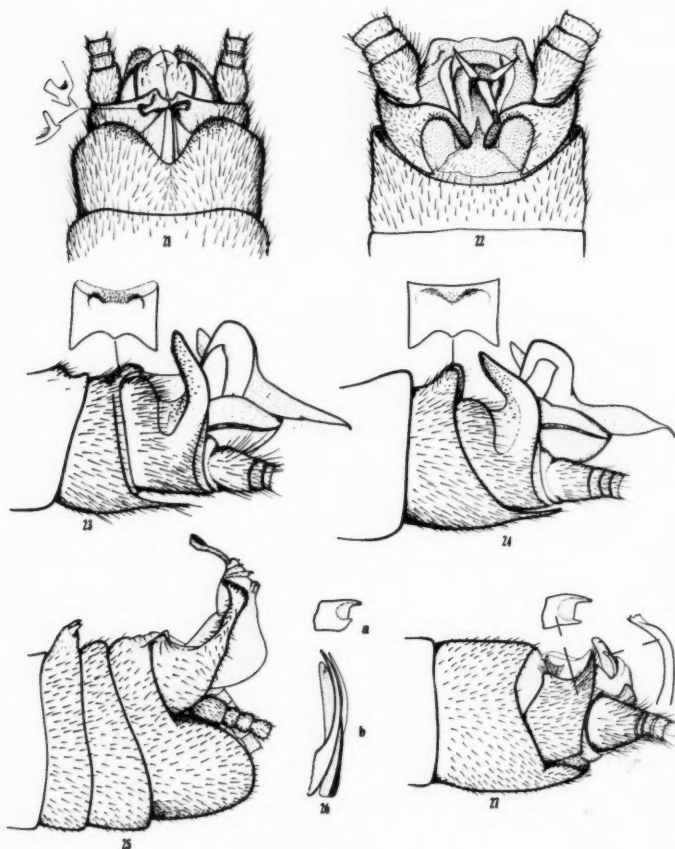
I am fully aware that in my work I am "standing on the shoulders of my predecessors." Therefore, I hope that any apparently excessive indulgence in criticism will be received in the constructive spirit in which it was given. Such criticisms and corrections are necessary for a full appreciation of the taxonomic status of the species concerned when there are errors in the literature, especially since it may not be the good fortune of future interested students to have the opportunity to study as many of the type specimens as have been available to me for this work.



Head color pattern of: (8) *A. picticeps*, (9) *M. signata*, (10) *P. aurea*, (11) *P. bradleyi*, (12) *P. tibialis*. Female subgenital plate of: (13) *A. curvata*, (14) *A. minor*, (15) *A. picticeps*, (16) *M. signata*, (17) *M. subtruncata*, (18) *P. aurea*, (19) *P. bradleyi*, (20) *P. tibialis*.



In the accomplishment of this work over the past two years I have been continually indebted to numerous entomologists. For the pleasure of studying the types of the species discussed above I am deeply indebted to Dr. Banks of the Museum of Comparative Zoology of Harvard, to Dr. Palm and Dr. Dietrich of Cornell University, and to Dr. Gurney and Dr. Chapin of the U.S.N.M. Without their kindly cooperation the pleasure of this work would



Male terminalia of: (21) *A. minor*, (22) *A. curvata*, (23) *M. signata*, (24) *M. subtruncata*, (25) *P. aurea*, (26) *P. bradleyi*, (27) *P. tibialis*. 26a is the dorsal lobe of the tenth tergite and 26b is the supraanal process and lateral stylets of *P. bradleyi*.

not have been mine. And without the advice and counsel of these men and especially the staff of this entomological department this work would have been much more difficult and less complete than it is.

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## The Invertebrate Population of a Central Oklahoma Prairie, November, 1933, to September, 1936

Martha W. Shackleford

In many communities, seasonal fluctuations in numbers of organisms repeat themselves yearly. For example, the yearly cycle is accepted as established for constituents of the marine plankton, such as diatoms, dinoflagellates, and copepods. The seasonal distribution of groups in the fresh-water plankton has received much study. By sweep-net catches in vegetation, such seasonal distributional data have been obtained for small arthropod forms in land communities (Summary in Carpenter 1936). The present study is another of this series; but differs from many others in being a grassland project.

### Location

The area of grassland where collections were made was fenced off from grazing during the winter of the first year of the study. It was a two-acre tract at the north end of the college farm, two miles west of the Oklahoma College for Women, Chickasha, Oklahoma. The field was level upland and had many buffalo wallows. During the rainy periods, the wallows became temporary ponds and, in the rainy spring of 1935, the whole area was covered with water for a period of ten days. During this wet spring, which came about the middle of the study, the field was an almost pure stand of *Thelesperma trifidum*. The principal grasses were *Andropogon saccharoides*, a species of *Paspalum*, *Hordeum pusillum*, and *Buchloe dactyloides*. The characteristic forbs were, in addition to the *Thelesperma*, *Aster multiflorus*, *Plantago Purshii*, *Ambrosia artemisiifolia*, *Amphiachyris dracunculoides*, and *Opuntia*. Collections were not made from the buffalo wallows. The area was a late seral stage of a secondary succession initiated by overgrazing, coming within the tall grass prairie (*Andropogon-Bison-Canis* Association, Carpenter 1939).

### Weather Conditions

The period of study covered two years of drought with a spring of heavy rainfall between. In 1934 the rainfall was much below normal from February through August. According to Climatological Data, '34, "the intense heat and deficient rainfall from mid-June to near the close of August resulted in one of the worst droughts of record for Oklahoma." In 1936, the rainfall was even farther from normal during the same period of spring and summer and temperatures were high. In Climatological Data, August, '36, conditions were described: "The intense heat of this month and that of July preceding, coupled with the marked deficiency of precipitation since January 1, led to the worst drought in State history and resulted in rapid deterioration

of all crops and a depletion of stock water and feed that caused much distress on Oklahoma farms." In the middle year of this study, 1935, in contrast to 1934 and 1936, rainfall was above normal in the vernal period, although in the estival period temperatures were high and rainfall scanty. In the pre-vernal period of 1935, occurred the most severe and general dust storms ever recorded for the state. An interpretation of the terms relating to seasons, such as pre-vernal, vernal, and estival, which are used in this discussion, is given in Figures 1 and 2. The hiemal season lasts from the killing frosts of November until the first trees blossom in the last week of February (an early sign of growth). The pre-vernal season continues from this date until the arrival of the heavy spring rains and the greening up of the grass in the last week of April. The vernal season runs from late April until the cessation of the rains about July 4. The estival season covers the hot, dry summer. The autumnal season begins with the break in high temperature and drought, which usually occurs in the first two weeks of September, and terminates with the killing frosts of mid-November.

### Methods

The sample in the herbs was fifty sweeps with a net of fourteen inches diameter. For the sod sample, a piece 12 inches by 6 inches, dug to a depth of 3 inches, was removed. Both samples were sorted in the laboratory of the Oklahoma College for Women. When the numbers of small ground forms were great, the soil was washed in small vessels. At other times, it was sorted by being spread in a thin layer. The results of the weekly collections are reported in Figures 1 and 2. During the last year, collections were made every two weeks.

### Total Herb Populations

Figure 1 graphs the total herb populations of the three years. The curves for the three years are similar in that they show two low periods and two high periods for each year. The low periods were in the hiemal and in the estival seasons. The high periods were in the vernal and the autumnal seasons, the autumnal peak not being as high as the vernal. In the cycle of herb numbers, the low population in the hiemal season, mounting through the prevernal, reached the yearly peak in the vernal, falling off again in the period of the estival society, and mounting to a second lesser peak in the autumnal society.

Figure 1 shows dissimilarities as well as similarities among the years in respect to total herb population. In the year of the wet spring, 1935, the vernal maximum continued well into the summer due to enormous numbers of a few species of Hemiptera, the principal ones being *Nysius californicus* Stal, which was correlated with the luxuriant growth of *Thelesperma*. On the basis of total herb population, it appeared that in wet years, the estival society might be divided into two periods, introducing a serotinal society to designate the late summer group, or more probably the vernal society might better be considered as continuing longer into July than in dry years.

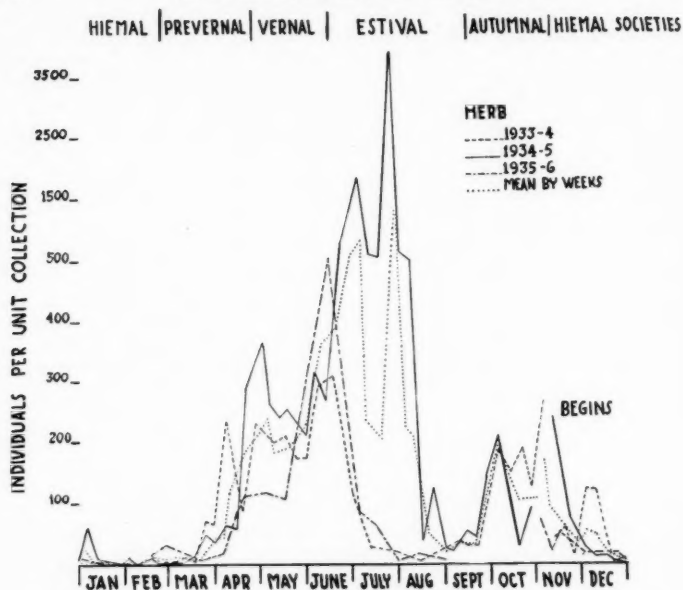


Fig. 1. Graph showing the total number in individuals in weekly collections of fifty sweeps, herb stratum, during the period beginning November, 1933, and ending September, 1936.

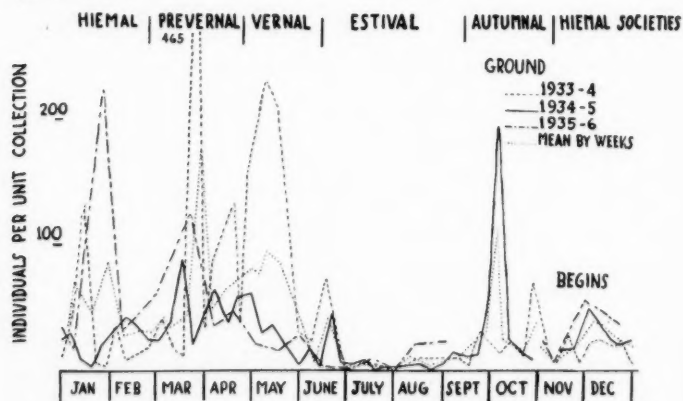


Fig. 2. Graph showing the total number of individuals in weekly collections of one-half square foot of sod, dug to a depth of three inches, during the period from November 1933, to September, 1936.

TABLE 1.—Fluctuations in Predominants, November, 1933, to September, 1936.

Predominants—numbers per 50 sweeps in the herbs or 1/2 square foot in the ground.	Hiemal Season			Prevernal Season			Vernal Season			Estival Season		
	1934	1935	1936	1934	1935	1936	1934	1935	1936	1934	1935	1936
1. Short-horned grasshopper nymphs	0	.1	.2	5	3.9	14.6	8	5.6	42.7	4.3	1.0	5.6
2. <i>Agallia sanguinolenta</i> Prov., leafhopper	.1	2.8	1.0	2.4	11.7	3.3	26.3	41.5	32.3	2.5	.1	2.4
3. <i>Collembola</i> , springtails	.1	8.0	14.0	.4	20.0	5.0	1.7	3.0	0	.1	.1	0
4. <i>Misumessus rosea</i> Key and Misumessus young, crab spiders	0	0	0	0	1.5	1.3	3.3	13.9	5.5	.2	17.5	.2
5. Aphididae	0	0	0	2	0	0	7.0	1.0	35.2	0	0	0
6. <i>Solenopsis molesta</i> subsp., ant	2.3	1.1	3.8	75.1	0	0	66.4	.4	.5	.3	0	0
7. <i>Nystus californicus</i> Stal., Hemiptera	0	0	0	0	0	0	.9	2.8	1.7	0	565.0	0
8. <i>Corizus lateralis</i> Say, Hemiptera	0	0	0	0	0	0	3.8	0	.3	0	0	0
9. <i>Polymerus basalis</i> Reut., Hemiptera	0	0	0	0	0	0	.4	29.5	0	0	14.5	0

Numbers 3 and 9 occurred in the ground. The remainder were herb forms.

The numbers per collection are the average of the weekly collections for each season. The duration of each season is shown in Figs. 1 and 2.

### Total Ground Populations

In the upper three inches of ground, Fig. 2, the fluctuations in total numbers from collection to collection were great. This lack of uniformity seemed to be due to the large number of niches in the ground stratum which presented greater variety than was encountered in the herb stratum. It was possible to make out the general direction of population trend. In the ground stratum, there was one high and one low period per year in each year studied. In general, the low period included the estival, autumnal, and early hiemal societies. The high period included the late hiemal, prevernal, and vernal societies. The highest ground populations were in the prevernal society.

It is evident that the population curves for the ground stratum do not coincide in shape with the herb population curves. In the ground, the time of highest population was through the winter and early spring—a time of low herb population. The autumnal period, which included one of the herb peaks, was a period of low ground populations in general. In the second year, one large collection occurred in October, when, atypically, an entire ant nest came within the upper three inches of soil in the sample. The herb population curve shows two high periods and two low periods per year; the ground, one high and one low. In the winter, when the herb population was low, the ground population was high. Also, in the autumnal period, the two strata were in contrast, the herb population being high and the ground low. However, in the vernal societies, both strata were well populated; and in the summer, after the end of the vernal peak, both strata were meagerly occupied.

In the first year, the ground population was highest due to a large number of ants of the *Solenopsis molesta* group. It was probable that the presence of these ants was due to the recent grazing in the area, and their partial disappearance in later years to the changes in vegetation resulting from the removal of grazing.

### Fluctuations in Predominants

The specific make-up of the community varied greatly in the three years. Table 1 shows the seasonal averages for nine of the very abundant species or groups. It would seem possible that there would be several groups of predominants; for example, (a) those prominent in all years, (b) those prominent in one year and of medium abundance in other years, (c) those prominent in one year and scarce in others, and (d) those prominent in one year and not taken in other years.

The predominants in this study fell into two main groups; the *stable predominants* which were of medium abundance in some years and in at least one year were conspicuously abundant; and the *unstable predominants*, which were scarce in one or more years, but abundant in at least one year. In Table 1, stable predominants were forms numbered one through five; unstable predominants were six and seven. *Corizus lateralis* Say and *Polymerus basalis* Reut. may represent a third type of predominant, which may be called a *variable pre*



*dominant*—apparently absent in one year and abundant in another year. It is noteworthy that no forms were of uniform prominence in all years. The less numerous invertebrates from this series of collections, as well as the predominants, are listed and their abundance is discussed in other papers. (Shackleford, 1934 and 1935.)

### Discussion

For the herb stratum of grassland, graphs showing seasonal abundance have been published by Shackleford (1929), Bird (1930), Hefley (1936), and Beed (1936). The first paper dealt with high and low prairies in east central Illinois, near Champaign. Bird worked on a "parkland prairie" near Birtle, Manitoba. Hefley studied seasonal changes in an edaphic subclimax prairie on the Canadian River flood plain in central Oklahoma. Beed showed data from June 11 to September 10 for a short grass area, the Niobrara Game Preserve, in north central Nebraska near the South Dakota border.

The form of the graph for the year 1935 in the present study resembles the graphs for the Illinois prairies and for the edaphic subclimax prairie. 1935 was a wet year and the Illinois prairie has a wetter climate than the area here discussed. The parkland prairie graph of herb population numbers is entirely different; beginning in June, rising to a peak through the summer, and ending in September. It shows no autumnal peak.

During the dry years, 1934 and 1936, in the present study, the vernal peak occurred at about the same time as did the maximum population in the short grass plains of Nebraska. Beed's study did not extend far enough into the fall months to determine whether or not a second peak would appear previous to hibernation in the short grasslands.

The form of the graph for seasonal abundance reported in this study is a common one for grassland herbal arthropods: two peaks and two troughs; low in the winter, increasing through the spring to a peak in the late vernal or early estival, declining through late July and August, and reaching a second period of abundance in September and October, just before the rapid decline to winter conditions.

This type of seasonal abundance is a common one outside the grasslands. For example, it is encountered in marine plankton studies, in the population of an Illinois Elm-Maple forest (Weese, 1924), and for an Oklahoma Prairie ravine (Potter, 1939, page 694). There is an increase in abundance with the advance of spring, a partial exhaustion and diminution of activity after the peak is past, a gathering together of forces for a second, usually lesser, peak just before the cessation of winter.

The inability of species in quantitative collections to maintain an equal numerical importance in succeeding years has been noted by Blake (1931) and Davidson (1932). They both stated that species abundant in one of the years were in some cases inconspicuous or wanting in the other year. The present study, carried through three years of contrasting weather, emphasizes

this instability of the predominants. Students of insects have long known of plague years of chinch bugs and grasshoppers. Fluctuations in numbers of other abundant arthropod forms is to be expected.

Fluctuations occur in the grasses and forbs of the prairies, especially when drought years are compared with normal years. These fluctuations are not so pronounced as are those of the arthropod predominants. It begins to appear that the amazing phenomenon will be to encounter an arthropod predominant whose numerical importance remains the same. Animal ecology, developing later than plant ecology, hoped in vain to find some abundant arthropods whose constant pressure upon the grassland would parallel in a certain sense the dominance of the grasses. It seems unlikely that such individual arthropod predominants exist. But the group of predominants taken as a group has a perennial integrity, as this study shows.

When a community study is in its early stages, abundant arthropods are called predominants. When more is known of their importance in interaction in the biotic community, some are designated arthropod influents and others, subinfluents (Shelford 1935). This is a wise practice, since it must be determined whether the predominants are stable, unstable, or variable before their influence upon the community can be established.

### Summary

1. The curve of weekly total herb population for a three year period in a poorly-drained, recently overgrazed grassland in central Oklahoma, shows two peaks—one in the vernal or early estival and one in the autumnal societies, and two low periods—one in the hiemal and one in the estival societies.
2. The ground population curve for the same period shows one peak in the hiemal and prevernal period, and one period of low numbers in the estival period.
3. When the numbers of individuals in a predominant species or group were compared in the three years, none were found to be abundant in all three years. Some were sufficiently evident in all years to be called stable predominants, and others were designated unstable predominants and variable predominants.

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## Studies on the Morphology of *Cystidicola* *cristivomeri* sp. nov.

(Nematoda: Thelaziidae) from the Swim Bladder of the  
Lake Trout, *Cristivomer namaycush* (Walbaum)

F. M. White and R. M. Cable

### INTRODUCTION

During the summer of 1940, a spiruroid nematode was found to occur in large numbers in the swim bladder of the lake trout, *Cristivomer namaycush* (Walbaum), from Flack Lake, Ontario, Canada. Further study revealed that the parasites represented an undescribed species of *Cystidicola* for which the name *Cystidicola cristivomeri* sp. nov. is hereby proposed. This paper presents a detailed study of the morphology of the new species. In a recently published abstract (White, 1940), the new specific name was withheld so that it would appear simultaneously with the publication of an extended account.

Species of *Cystidicola* have been reported from a great variety of localities. Of the fifteen described species, two have been reported from continental Europe and Asia, one from the Belgian Congo, six from Japan, three from Canada, and three from the United States. The usual site of infestation is the swim bladder; six species are stated definitely to occur in that organ. Others, however, have been reported from the oesophagus, stomach, intestine, and even in the body cavity and heart.

### HISTORICAL REVIEW

The first species of *Cystidicola* was reported almost a century and a half ago by Fischer (1798) who described and figured a nematode living in the swim bladder of trout. For this worm Fischer proposed the name *Cystidicola farionis*. Since that time, the species has been reported on several occasions and allocated to various genera. Its taxonomy has been reviewed by Shipley (1908), and Leiper (1908) has pointed out that since Fischer designated the worm as *Cystidicola farionis*, this name has priority and therefore must be considered valid. Another species, which Schneider (1866) described as *Ancyracanthus impar*, was placed by Railliet (1916) in the genus *Cystidicola*. Baylis (1934) regards this species as synonymous with *C. farionis*.

The third species of *Cystidicola* was described by Leidy (1886) as *Filaria stigmatura*. This particular form was placed in the genus *Cystidicola* by Ward and Magath (1917). It was described as a new species, *C. canadensis*, by Skinker (1930) who later (1931) decided that the species was not new but actually *C. stigmatura*. Wright (1879) described another species, *Ancyra-*

*canthus serratus* which Railliet (1916) regarded as possibly a species of *Cystidicola*. Linton (1905) described and named *Filaria galeata* which has been transferred to the genus *Cystidicola*. Ishii (1916) reported a new species, *Ancyracanthus salmonicola*, which Fujita (1927) placed in the genus *Cystidicola*. Fujita (1920) described a new species, *Spiroptera salvelini*; he later (1928) transferred this species to the genus *Cystidicola* and described a new species, *C. iwana*. In 1933, two new species were reported, *C. lepisostei* Hunter and Bangham and *C. skrjabini* Layman. Rodhain and Vuylsteke (1934) described the new species, *C. minuta* and Ekbaum (1935) reported *C. walkeri*. Fujita (1939) described *C. brevicauda* and later (1940) the new species: *C. chitosensis*, *C. mesopi*, and *C. minuta*. Since the last name is preoccupied by *C. minuta* Rodhain and Vuylsteke (1934), Fujita (1941) has renamed the species *C. chika*.

#### MATERIALS AND METHODS

Lake trout were caught, the swim bladders were opened, and the worms transferred to isotonic saline solution for at least ten minutes. The solution was then decanted through a cloth screen and the worms killed in hot glycerine-alcohol solution (96 parts of 70% alcohol and 4 parts of glycerine). This solution served as a preservative and later as a clearing medium upon the evaporation of the alcohol, bringing the worms gradually into pure glycerine. Several specimens were cleared in lactophenol. To study the buccal armature from an *en face* view, the anterior ends of worms were removed and mounted vertically in glycerine-jelly. These preparations were covered with a no. 1 cover glass and observed with the oil immersion objective since high magnification was necessary to determine minute details of oral structure.

All observations were made on preserved material and measurements are in millimeters. Figures were drawn to scale with the aid of a camera lucida and a microprojector.

#### OBSERVATIONS

##### *Cystidicola cristivomeri* sp. nov.

*Specific Diagnosis*.—Slender, elongate spiruroid with characters of the genus. Cuticle with longitudinal striations. Anterior end bluntly rounded, 0.053-.055 in diameter. Reproductive system meager, filling only small part of body cavity. Oral opening elongate dorsoventrally, constricted by a pair of prominent lateral teeth. A dorsoventral pair of teeth and small labial teeth, 4 in each quadrant formed by dorsal, ventral, and lateral teeth. A pair of lateral ridges each bearing a papilla. Other papillae lacking. Stoma 0.17-.18 long and 0.025 wide posterior to middle. Esophagus with anterior muscular portion 0.29-.35 long and posterior glandular region 1.37-1.39 long. Nerve ring 0.3-.31 from anterior end of body.

*Males*.—Length 15-21, average 19.7; width 0.20-.27. Anus approximately 0.173-.175 from tip of tail. Tail spirally coiled, averaging one and one-quarter turns. Spicules very unequal; short right one 0.14-.16 long by 0.0118

in width at distal end, 0.023-.036 at proximal end; the long, left spicule 0.63-.77 in length, sharply pointed distally, and 0.0118-.0125 wide near proximal end. 5-9 double pairs and one single pair of preanal papillae; 5 pairs of post-anal papillae, the second and third forming a double pair.

*Females*.—Body length 23-32, averaging 26.7; maximum diameter (near vulva) 0.69. Vulva slightly posterior to middle of body. Vagina 0.424 long, approaching the vulva posteriorly. Uteri divergent. Mature eggs 0.043-.048 in length by 0.025-.039 in breadth, lack polar filaments and when fully formed, always with a "lateral" pair of conspicuous, longitudinal, mammillated ridges, and less regularly polar masses of similar proteinaceous material.

Host: *Cristivomer namaycush* (Walbaum).

Site: Swim bladder and *ductus pneumaticus*.

Locality: Flack Lake, Ontario, Canada.

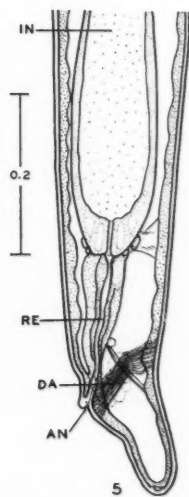
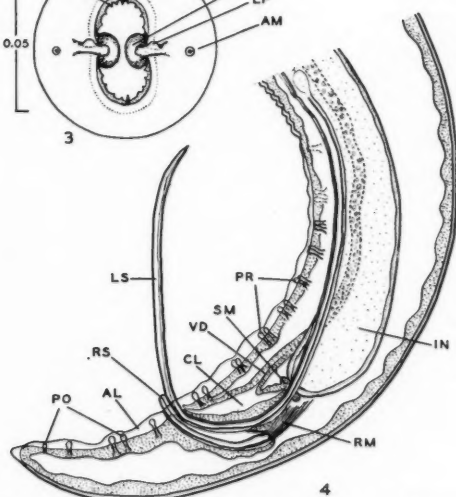
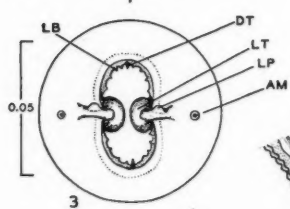
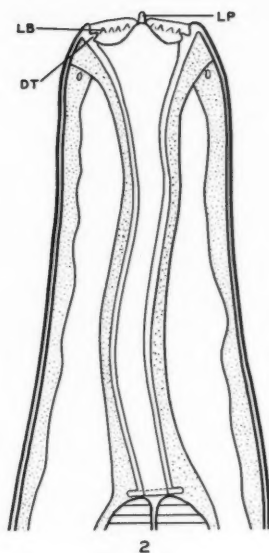
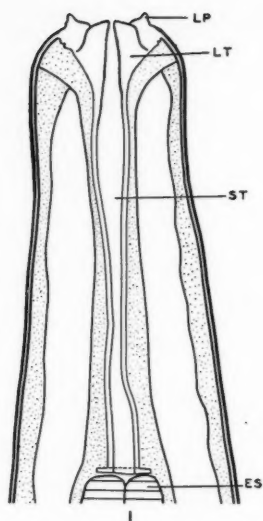
*Observations*.—The cephalic structures, typical of *C. cristivomeri*, can be seen clearly in an *en face* view (Fig. 3) with the oil immersion objective. The oral opening is dumb-bell shaped, being constricted by the pair of large lateral teeth. These structures are angular in dorsal or ventral aspect (Fig. 1), but in lateral view (Fig. 2) appear conical with blunt tips. They merge into the cuticular lining of the stoma. From each tooth a ridge extends laterally towards the external amphids, blending into the cephalic cuticle. Each ridge bears a conical papilla. Fig. 3 shows the papillae as observed when deflected by cover glass pressure. The dorsal and ventral teeth are nearly as small as the sixteen labial teeth. There are four labial teeth irregularly spaced in each quadrant formed by the paired lateral and dorsoventral teeth. The large lateral teeth appear chitinous, while the dorsal, ventral, and labial teeth have the appearance of papillae.

The chitinoid lining of the stoma has many fine horizontal striations. In dorsal aspect the stoma is nearly uniform in width (Fig. 1), but is observed in lateral view (Fig. 2) to flare toward the mouth.

Because of its simplicity and meagerness, the reproductive system can be followed with ease in whole mounts. The ovaries are slender and tubular and become even narrower before joining the oviducts. Each ovary has at its tip a prominent cap cell which contains a large vacuole. This vacuole presses the nucleus of the cell against the blind end of the ovarian tube. The oviducts are slender tubes also, but have thick walls and a narrow lumen. As the germ cells pass through the oviducts in single file, they are compressed until cylindrical in shape. At the junction with the uterus, each oviduct is provided with a distinct bulb-like sphincter. At the end joined by the oviduct, each uterus is expanded and filled with cells. These cells are glandular in appearance but may be accumulated germ cells. In immature females, however, the presence of these

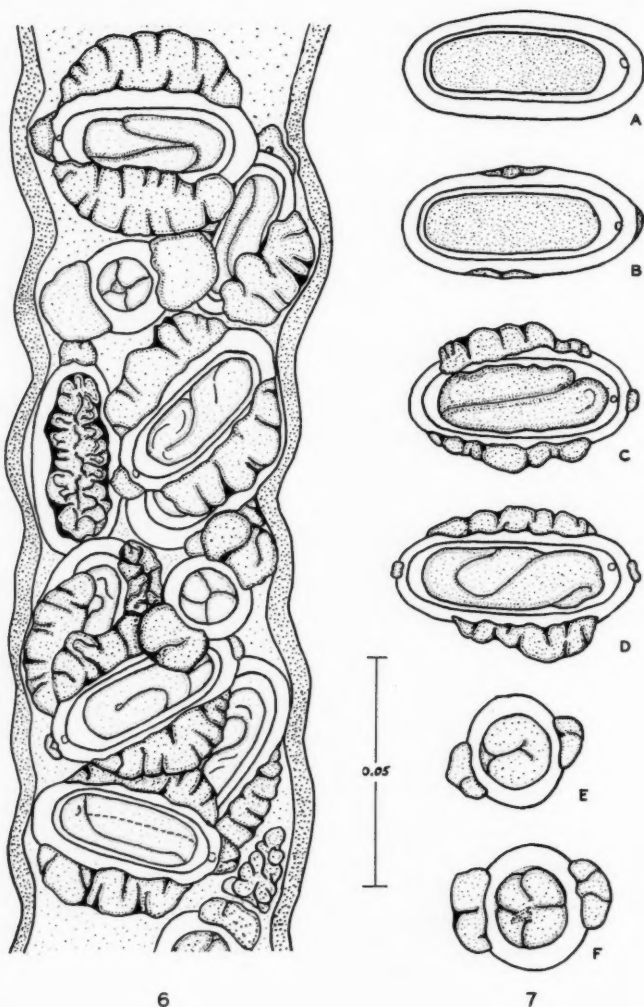
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Figs. 1-5 (All figures concern *C. cristivomeri*): 1. Ventral view of anterior region. 2. Lateral view of anterior region. 3. *En face* view of anterior end. 4. Posterior end of male. 5. Posterior end of female. Lettering: AL, caudal ala of male; AM, amphid; AN, anus; CL, cloaca; DA, depressor ani; DT, dorsal (or ventral) tooth; ES,



esophagus; IN, intestine; LB, labial teeth; LP, lateral papilla; LS, left spicule; LT, lateral tooth; PO, postanal papillae; PR, preanal papillae; RM, retractor muscle of spicule; RE, rectum; RS, right spicule; SM, sphincter muscle; ST, stoma; VD, vas deferens.





Figs. 6-7: 6. Portion of uterus of *C. cristivomeri* showing eggs in situ. Stages in the formation of eggs, showing the gradual formation of mammillations; E and F, end views of stages shown in C and D.

cells in the enlarged end of the uterus indicates that they are glandular in nature. Beyond this region each uterus becomes narrower for a short distance and the contained eggs are first seen to have distinct chitinous shells (Fig. 7a). Beyond this region, the uterus widens, the breadth remaining fairly uniform until the vagina is approached.

As the eggs pass through the uteri, the characteristic proteinaceous mammillations become more and more pronounced (Fig. 7 b-f). The "lateral" mammillations first appear as thin plaques on the shells of eggs containing embryos in late cleavage stages. By the time the larvae are well developed, these mammillations are completely formed. The polar mammillations are not as characteristic or as regularly formed, being conspicuous in some eggs and absent at one or both poles of others containing fully developed embryos. As they approach the vagina, the eggs pass single file through the uteri.

From the vulva, the vagina extends obliquely posteriad for about half its length, then bends at a right angle and joins the uteri. This flexure, dividing the vagina into two parts, is marked by a valve-like modification of the dense cuticular lining found in both parts of the vagina.

The anterior ovary originates at the beginning of the second quarter of the worm and extends posteriorly. The anterior uterus extends posteriorly a short distance beyond the vulvar region, where it makes a simple loop and then passes anteriorly to the vulvar region, curving backward to join the vagina.

The posterior ovary originates in the third quarter of the body and the oviduct extends backward into the posterior quarter, twisting about the swollen parts of the uterus which it joins after bending anteriorly. About halfway to the vulvar region, the posterior uterus usually loops backward and then forward before proceeding directly to the vagina. The relationships of these parts are subject to considerable variation, depending on the degree of maturity. In one atypical specimen, the uteri were opisthodelphic rather than amphidelphic.

The male reproductive system is very simple. It consists of a single testis which originates in the posterior half of the body. The testis extends as a straight narrow tube into the last quarter of the worm where it makes a simple loop and then proceeds posteriorly to the vas deferens. The vas deferens is thick-walled and about equal to the length of the spirally-coiled portion of the caudal region (Fig. 4). The long, left spicule is sharply tapered at the end but broadens gradually into a V-shaped trough. The alae are wide, extending dorsally over half the width of the tail. The free edges of the alae frequently are undulant and contain many small, spherical bodies, which are variable in size and resemble oil droplets.

#### DISCUSSION

*C. cristivomeri* differs from other described species of *Cystidicola* in several respects, especially the nature of the egg. The mammillations, characteristic of the egg, have been reported for only one other species, *C. minuta* Rodhain and Vuylsteke, 1934. The eggs of *C. minuta* have lateral "floats" with even contours, and "dorso-ventral" protuberances, and are illustrated as extending through the chitinous shell, while the "lateral" mammillations of *C. cristivomeri*

eggs are coarsely rugose, polar mammillations are usually present, and "dorso-ventral" mammillations are lacking; also egg size, and body length are significantly greater in *C. cristivomeri* than in *C. minuta*, the females of *C. cristivomeri* being five times as long as those of *C. minuta*. The absence of filaments on eggs of *C. cristivomeri* distinguishes this species from those having filamentous eggs, viz., *C. farionis* for which Berghe (1935) has described lateral as well as polar filaments; *C. mesopi*; *C. minuta* Fujita; *C. scerrata*; *C. salmonicola*; *C. skrjabini*; *C. stigmatura*; *C. walkeri*. Polar filaments are absent in all other species of *Cystidicola* but mammillations are lacking except in *C. minuta* Rodhain and Vuylsteke and *C. cristivomeri*. Species which have nonfilamentous eggs may be differentiated as follows. Postanal papillae are lacking in *C. chitosensis*. The anterior end of *C. cristivomeri* is small and tapering as compared to the cushion-like cephalic hood on *C. galeata*. Male and female lengths of *C. iwana*, are less than in *C. cristivomeri*, while their eggs are longer and thinner shelled. *C. lepisostei*, has only six double pairs of preanal and five single postanal papillae, whereas *C. cristivomeri* has from five to nine double pairs of preanal, and five pairs of postanal papillae, of which the second and third form a double pair. The males and females of *C. salvelini*, are also small in size and the male has only four pairs of preanal and five pairs of postanal papillae.

It is interesting to note that the present species was not reported by Hunter and Bangham (1933) who made an extensive study of fish parasites of Lake Erie. The high elevation of Flack Lake and numerous falls between it and Lake Huron probably have long isolated the fishes of that region from those in the Great Lakes. This would account for the apparent absence of these parasites in lake trout from the Great Lakes.

The lake trout, being a physostomatous fish, that is, having a functional *ductus pneumaticus* between the swim bladder and alimentary canal, the eggs and even worms probably pass through this duct into the intestine and escape from the body.

From what is known concerning the life history of other spiruroids, the eggs of *C. cristivomeri* probably are ingested by arthropods in which the larvae develop to the infective stage. Fishes probably obtain the worms by eating infected arthropods, the young worms being digested from the intermediate host and making their way into the swim bladder of the fish by way of the *ductus pneumaticus*. In view of the migratory habits of certain nematodes, it is possible that the larvae may penetrate the intestine of the fish, pass through the body cavity, and bore into the swim bladder.

#### SUMMARY

A new spiruroid nematode, *Cystidicola cristivomeri* sp. nov., is reported from the swim bladder of the lake trout, *Cristivomer namaycush* (Walbaum). This nematode is described and compared with other species of *Cystidicola*.

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# Collecting Microfossils<sup>1</sup>

Hubert G. Schenck and Robert T. White

## Introduction

Much has been written on the collection, preparation, and preservation of plant, vertebrate, and larger invertebrate fossils. Relatively little has been published, however, on the subject of the systematic collection of the smaller invertebrates, generally microscopic in size. Yet such fossils as foraminifers, diatoms, fish scales, and ostracodes have proved to be of great value in the detailed correlation of strata within a limited area such as an oilfield, a basin of deposition, or a whole geologic province. These fossils are also valuable in ecologic and evolutionary studies. The reason for their value is that the microscopic fossils are usually much more abundant in many strata and are better preserved than the larger fossils. Also, many specimens of different species of minute fossils may be obtained from well cores or cuttings, whereas one is fortunate to obtain rare fragments or, at best, relatively whole specimens of mollusks or other larger fossils from subsurface samples.

In view of the proved importance of the smaller fossil organisms as an aid to stratigraphic geology and paleontology, this paper aims to supplement the literature dealing with their classification and stratigraphic occurrences by pointing out the necessity of adopting systematic methods of collecting sequences of fossiliferous samples. The need of precisely locating collecting stations both stratigraphically and geographically is emphasized, for the value of interpretations drawing upon paleontologic evidence is directly proportional to and is limited by the care exercised in the collection and allocation of samples.

Further, this paper gives the field geologist some notes on practical methods for the collection, labelling, and stratigraphic and geographic allocation of fossiliferous samples. We do not presume to be presenting either original or indeed the only workable ones. Rather we discuss a number of successfully employed procedures and leave the ultimate choice to the individual collector, who is the best judge of his own requirements.

In this report we are biased by our experience with the use of microfossils in petroleum geology. We are primarily interested in the collection of orderly, stratigraphically arranged sequences of fossiliferous samples. The methods discussed herein are applicable not only to those branches of geology directly concerned with the exploitation of materials from sedimentary strata but also to interpretive geology and paleontology.

<sup>1</sup> This article is a sequel to "Applied Paleontology" by Hubert G. Schenck, *Amer. Assoc. Petrol. Geol., Bull.* 24(10):1752-1779, 5 figs., 3 pls., November, 1940.

### Objectives of Collecting

The ultimate objectives for collecting microfossils in economic geology are the determination of the age of the strata by paleontologic criteria or the determination of the relative stratigraphic position of the fossiliferous strata as compared with other geologic sections. Both objectives frequently constitute a single goal. Microfossils have proved to be of great value as an aid in deciphering the detailed structure of an area and in facilitating the precise correlations demanded in economic work. Here are a few of the ways in which microfossils can be used:

1. Microfossils are helpful in the correlation of a specific geologic section with one or more surface or subsurface sections.
2. The age of a sandstone lens in a thick shale section often can be determined with the assistance of foraminiferal evidence from the enclosing shales.
3. The relative magnitude of a hiatus is frequently disclosed by micro-paleontologic data.
4. In thick sections where fossils are numerous and where the samples are carefully collected, microfossils may provide the necessary control for the measurement of fault displacements.
5. Microfossils supply in many cases the paleontologic data necessary for setting up a complete zonal classification of a total section ("standard section") of strata.
6. The study of facies is often aided by attention to microfossils.
7. The small fossils can sometimes be used to determine whether a lithologic facies transgresses zonal boundaries; for deciding, for example, whether a given sand occupies different stratigraphic positions in the section areally or whether its contacts parallel a faunal horizon.

Such a list of uses suggests a grouping of the application of microfossils to stratigraphy under two main heads: (1) microfossils as a phase of paleontology and (2) microfossils as a phase of lithology. Thus, outcrop-to-well correlations, the stratigraphic position of a sand unit in a shale, and the thinning and thickening of formations are local problems in which microfossils are used more as distinctive ingredients of the rocks than as markers of geologic time. On the other hand, the collection of microfossils for the purpose of setting up a zonal<sup>2</sup> classification of strata—a classification which is independent of changes of lithology—would fall into the first category.

Another reason for collecting microfossils is in order to obtain data upon which to found inferences concerning environmental conditions during past geologic epochs. Paleoecologic studies, which are receiving increasing attention among scientists, emphasize the intimate relation between the fossils and the entombing sediments.

<sup>2</sup> We are here using the term Zone in the strict sense. See Schenck and Muller (1941).

An important objective is the collection of samples for paleontologic research. Frequently large quantities of material are collected in order that the worker may have sufficient specimens to determine the ranges of variations of species, the probable lineage of fossils, or other paleobiologic matters. Type localities of species may be visited for the purpose of obtaining topotypes. A few persons throughout the world obtain material for commercial supply houses which, in turn, sell specimens to museums, universities, and to other purchasers. The exchange of material is a general practice among paleontologists. These are among the many examples of the collection of microfossils as a phase of paleontology.

### Control Section

The term *control section* is used widely among professional stratigraphers to designate a surface or subsurface section which has been measured so accurately, described in such detail, and so closely sampled that it may be used for local correlations or for paleoecologic inferences. For example, if an oil company contemplated drilling a well at a certain spot in the San Joaquin Valley, California, the geologist would be charged with the task of preparing a control section at a nearby locality. This might necessitate the detailed study of the outcrops in the hills west of the proposed site, or if a well had been drilled previously near the new site, then that well, if adequately studied, would be the control section. The newly drilled well, in turn, would become a control section if detailed stratigraphic data are obtained from it.

Numerous examples might be given of the use of control sections in interpretive geology. An excellent one is the detailed study by Natland (1933) whose comparison of carefully collected Recent foraminiferal assemblages with well allocated fossils permitted him to infer the probable depth and temperature conditions under which were deposited the Pliocene and Pleistocene marine strata in the vicinity of Ventura, California.

Finally, control sections are necessary for the establishment of Zones. As an illustration, consider the Reliz Canyon section described by Kleinpell (1938). This section gave him the stratigraphic control requisite for a local biostratigraphic classification. Additional sections elsewhere provided the basis for extending this classification throughout the Californian geologic province. The two papers by Adams (1939, 1940) will also be referred to by one who is interested in the use of microfossils in zonal paleontology.

### Collecting Outcrop Samples

*Introduction.*—This report is separated into two main divisions, the collection of outcrop samples and the collection of well samples. In the discussion of methods of collecting outcrop samples, emphasis is placed on the methods dealing with continuously sampled surface sections in which the paleontologist is interested. Many of the methods are equally applicable, however, to the collection of individual samples which are of value to the field geologist as an



aid in mapping. The importance of collecting sequences of properly allocated samples cannot be stressed enough.

It is the strong conviction of many stratigraphers that geologic mapping should precede the collection of outcrop samples. Such mapping serves to furnish a structural and stratigraphic picture of the local area and generally provides a better basis for determining the true thicknesses of the strata than does the measurement of a single, isolated section. Moreover, mapping frequently discloses which sections are best to sample. Certain parts of a sequence of strata may be especially suitable for this purpose because of the locally well-preserved fossils, while if one selects a section merely because of completeness he may find that it is barren. This might lead to the erroneous conclusion that the entire sequence in that region is barren. Frequently abundant fossils are found in strata in a local area, yet the same lithologic unit may be barren along the strike. Geologic mapping thus aids in selecting the fossiliferous sections.

An alternative procedure is to sample a series of carefully measured sections and then later to tie them in by geologic mapping. The chief objection to this method is that it is too time-consuming. It is sometimes necessary, however, to sample a section before the mapping of the area has been completed, and in reconnaissance investigation it is helpful to measure a section or several sections before mapping.

*Field equipment.*—Equipment for sampling a section should include maps, surveying instruments, hand lens, sample containers, and tools for collecting samples.

The maps should be of large enough scale to enable one to plot on them each collecting station. They may be large-scale topographic maps or airplane photographs, preferably containing on them all available geological information.

The choice of surveying instruments is determined by the detail and accuracy demanded. It is advisable to use an alidade or transit where great detail is desired, where the attitudes of the beds are variable, where the section is long, and where discontinuous outcrops necessitate offsets. On the other hand, on a well-exposed homoclinal section or one in which there are a number of "marker" beds to aid offsetting, a Brunton and tape measurement is generally satisfactory. It is often sufficiently accurate to measure the stratigraphic distances between the collection stations from their plotted locations on a large-scale topographic map or on an airplane photograph if the distortion of the base and the degree of slope of the ground surface are known.

A good hand lens is useful in looking for fossiliferous beds to sample and in making lithologic descriptions of the sedimentary strata in the field. In the hands of a skilled collector the hand lens reduces the bulk of material to be handled in the laboratory, thus concentrating the work of the laboratory on the more fossiliferous samples, and increases the chances for obtaining good material in the field. The amount of magnification depends on the nature of the examination. A 10- or preferably a 14-power lens has sufficient magnification

to reveal the presence of microfossils, and its large field of vision makes possible a rapid examination of a sample. A 20-power lens is valuable for the identification of individual microfossils, but the small field of vision decreases its value for rapid examination of samples.

Many types of sample containers are in use, the particular kind depending chiefly on climatic conditions. One commonly used by oil companies in dry regions is illustrated in Figure 1. Heavy manila paper and stapled seams make

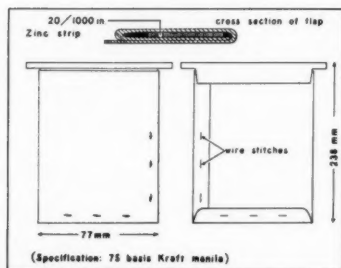


Fig. 1.—Plan of one widely used sample bag. Locality and other data may be printed directly on envelope. Data recorded on fold-over flap will not be lost through chafing, tear, or other wear.

this bag strong enough to be subjected to some moisture without breaking open. The fold-over top makes a convenient seal. In moist climates a muslin or canvas bag with a cloth label stitched to one of the sides and with a draw string top is more satisfactory. Figure 2 is an illustration of a kind in general use on the Gulf Coast. A heavy canvas bag is also preferable when the samples are subjected to much buffeting before reaching the laboratory. In wet climates it may be necessary to use tin or wooden containers such as boxes, tubes with screw top lids, or cans with secure tops. If these types of containers are not available, a heavy paper bag, such as a nail bag, or various kinds of tins and jars can be substituted.

Information regarding the number, geographic and geologic location, lithology, and nature of the fossils is usually written on the outside of the sample bag. Another practice is to record this information on a field label inserted in the container with only the sample number with the name and number of the section printed on the outside of the container to aid in arranging the samples in the laboratory. If canvas bags or tins are used, field data should be printed with indelible or hard pencil on cloth labels which are inserted either with the samples or tied on the outside. A detailed description of field labels and methods of labelling sample bags will be given later. The emphasis here is upon this direction: Place the samples in well identified containers which will not leak nor allow the sample to be contaminated or lost.

The choice of tools required for the collection of samples is governed by the amount of soil to be moved in order to obtain fresh, unweathered material. A geologist's pick is adequate if the outcrops are free of weathered material. A thin soil mantle can be readily scraped aside with a hoe. Some oil company stratigraphers in California carry, in preference to a pick, a hoe with a five-foot handle which is marked off in feet and can thus be used as a measuring instrument as well as a tool for collecting material. In areas where the soil cover is not too thick the unweathered formation may be exposed continuously in a trench dug with a pick and shovel. Where the soil mantle is thick, pits may be dug at intervals or a post-hole augur may be used in order to get fresh samples.

*Factors governing the sampling of a surface section.*—The general location of a section to be sampled is selected by the geologic or paleontologic staff of an oil company, or both. The exact position of the section is determined by such considerations as quality of exposures, structural features, and accessibility. Some oil companies require that a geologist and paleontologist collect the section together. The assumption is that the geologist, by virtue of his field work, has a more intimate knowledge of the stratigraphy and is able to select the best possible section to sample. Further, it is of value to the paleontologist

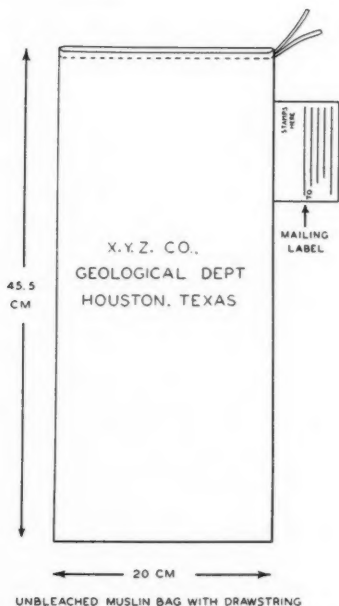


Fig. 2.—Muslin collecting bag used on Gulf Coast.

to draw upon the geologist's knowledge of the field relationships of the strata from which his samples are collected. Some companies leave the task of collecting surface sections to the geologists, while in other companies it is handled by the paleontologist. The decision regarding the section to be sampled and the personnel to do the job will thus vary with the company.

The section to be sampled is laid out as closely as possible normal to the strike of the beds. This is for convenience and accuracy in measuring the thickness of the strata. The section is along one continuous line if that is feasible. Slides, deep weathering, or alluvium, however, commonly necessitate the making of a number of offsets. These offsets can frequently be made along "markers" such as bentonite, limestone, or sandstone beds. Short offsets can, in fact, be made along any stratum that varies enough from the predominant lithology of the section to be traceable. In a homogeneous shale unit, the offsets should overlap one another so that the collected microfossils themselves can be used in correlating the offset beds. Such matters as these are taken into account before the actual sampling of the strata is undertaken.

The stratigraphic interval at which samples are taken is governed by a number of factors. Suppose that reconnaissance work has shown that paleontologic divisions of the strata can be recognized and that these divisions are only a few feet in thickness. In such a case the samples must be closely spaced, stratigraphically speaking. A closely sampled control section in an area may furnish a clue as to how closely subsequent sections should be sampled. The sample interval may be based on company policy, on the judgment of the collector, or on that of his superior. The interval depends largely upon the area and the degree of refinement desired, it being borne in mind that no correlations of strata can be more accurate than the accuracy of the stratigraphic sections which are being correlated. A large factor is the laboratory facilities for preparing and studying the samples.

One common procedure in California is the spacing of samples in a shale section 25 feet apart stratigraphically, with closer sampling immediately above and below "marker" beds or near the contacts between rocks of different lithologic character. One company with a large staff may arbitrarily take a sample every 10 feet; another takes some material throughout a thickness of 10 feet, a "composite sample," and sets a numbered stake at every 10 foot interval; and a third organization may insist that the collector make a detailed hand lens examination of the rocks and collect samples only where microfossils were observed, as it is felt that a careful, experienced collector can save a tremendous amount of costly laboratory tedium. A variation of this is to collect the samples in which microfossils are apparent and, if the samples are widely separated stratigraphically, to collect other samples in between so as to fill out the section. Sometimes it is imperative to sample the rocks every few inches. No set rule can be given regarding the stratigraphic interval for sampling. Much judgment, based upon experience, must enter into the collection of a section. Experience has taught that surveys of third-order control do not aim at first-order accuracy.

Locally other factors may govern the sampling of surface sections. Hans E. Thalmann, after reading the typescript of this article, emphasized the factor of adequacy of sample. He pointed out that geologists in the humid tropics often collect material in out-of-the-way spots to which it may be difficult and costly to return. The collector, if he has transportation facilities, is urged to satisfy the paleontologist by giving him abundant specimens.

*Measuring and sampling a surface section.*—The following is an example of the procedure followed by a collector in measuring a section directly from a map: First he found a place where the soil cover was at a minimum, a gully and a steep hill slope in this instance. On his map he labelled the section "A." As the determined sample interval was too small to permit the plotting of every sample station on the map, he plotted the locations of the samples only where the line of section made a bend, as at the bend in the gully, or where good physical features enabled him to locate accurately the position of the particular sample. The material taken between the sample stations which were plotted on the map were labelled on the bag and in the notebook as being a certain number of feet from the plotted station. Thus, sample 2 was 45 feet from sample 1, and sample 3 was 30 feet from sample 2. Where samples were only a few feet apart, however, the collector estimated directly the stratigraphic interval separating them from preceding samples. Since he used an airplane photograph, the angle of slope was indicated between the samples together with the dip of the strata in order that the stratigraphic thickness between the two horizons might be computed accurately. Section corners and prominent hill tops were plotted on the map.

The collector found it advantageous to draft a rough columnar section in his field note book as the samples were taken. On this column he showed graphically the lithology of the strata and the positions of the samples with respect to the lithology. This column, sketchy though it was, proved to be of considerable aid when the final geologic column was drafted in the office.

The following is an example of a section measured and sampled under plane-table control.<sup>3</sup> The section began at the base of Miocene non-marine beds where a stake was set and numbered "O." A few feet stratigraphically lower another stake was set and numbered "1." Here a fossiliferous sample was collected and given the same number. Below this stake other samples were taken at intervals of 3 feet stratigraphically. These were labelled "1-3," "1-6," "1-9," and "1-12." At a distance of 15 feet below sample "1" was the top of a massive sandstone. A stake numbered "2" was set here to mark the top of this lithologic unit. The sandstone was 50 feet thick, and another stake ("3") marked its base. Two feet stratigraphically below the sandstone the observer noted fossils, so he collected a sample and numbered it "3-2." This system was followed for the entire section. Each formational contact was surveyed for a short distance on each side of the line of section and numerous

<sup>3</sup> The plane-table is used in some regions to the exclusion of other instruments. For this reason we give bibliographic references to the more important papers in English on this topic.

dips and strikes were recorded. Significant cultural features, benchmarks, section corners, and other features were shown on the map.

Adequate notes on the lithology of the strata should be taken, no matter whether the rocks carry fossils or not. Distinctive lithology is often of great value in correlating one section with another. For example, a bed of bentonite may occupy a constant stratigraphic position over a considerable area. A gray sandstone with abundant micas may occur lower stratigraphically than a gray sandstone lacking micas. An oölitic limestone about fifty feet thick served as a useful "key bed" in one area; a foraminiferal reddish brown shale proved to be an excellent marker bed in another. When time and weather prohibit detailed descriptions in the field, rock samples should be taken for subsequent examination in the laboratory.

There are many reasons why it is important to give detailed lithologic descriptions of the strata. The use of lithology in local correlations is only one. The petroleum geologist is interested in permeability and porosity of sands which may form an oil reservoir on some buried structure. Other geologists are interested in the economic value of certain types of sedimentary deposits. Economic geologists are joining the research geologist in determining the relationships of faunal and lithologic facies because they appreciate the significance of interpreting geographic and ecologic changes.

Several geologists have pointed out that the plane-table is of limited value in little developed areas in the humid tropics, especially in lowlands where visibility is restricted by dense undergrowth. Mapping for oil companies in such areas is frequently carried on by means of a compass-steel tape series of traverses or polygons, tied into a trigonometric network set up by engineers by means of transit.<sup>4</sup> The network in such surveys is frequently of a general nature, for extreme accuracy is rarely required in the early stages of geologic exploration.

In areas where steeply dipping strata outcrop in a hilly terrain or where horizontal strata outcrop on the face of a cliff or a steep hillside, the thickness of exposed beds can be scaled off accurately with a measuring stick.

The "Jacob staff" method, which has been described by Blackwelder (1913), was employed by Olaf P. Jenkins<sup>5</sup> in some of his work, the results of which checked out closely with later drilling. The idea is simple. One places the end of a five-foot stick or hoe handle on the surface of a stratum, holding it at right angles to the bedding plane. Then one sights from the upper end of the stick to the ground along a line of sight which is at right angles to the stick (that is, parallel to the bedding plane). The collector continues somewhat as in Locke hand-levelling. More accurate results are obtained when a Brunton is attached to the staff and the level bubble is set for the angle of dip, but accurate work can be done rapidly without the instrument. The method is illustrated in Figure 3.

<sup>4</sup> Comment by R. Wright Barker, February 24, 1941.

<sup>5</sup> Letter dated August 11, 1941.

Before going into the field Jenkins prepared a form for the purpose of filling in the stratigraphic column on a scale of 100 feet to the inch. The only information recorded was the stratigraphic column, no altitudes, angles of slope, or other data being necessary. Occasionally, at critical places, he set marked surveyor's stakes in the ground for future reference.

Max B. Payne<sup>6</sup> points out that in measuring long sections by the Jacob staff or hoe-handle method some error is bound to occur. All sections should be checked by calculations from the map and the probable percent of error should be recorded on the graphic log of the section. Moreover, this method requires practice if it is to be used successfully and necessitates constant checking of the strike and dip with the Brunton compass, for even with well-exposed outcrops the sampler may deviate to some extent from the required normal to the strike and dip.

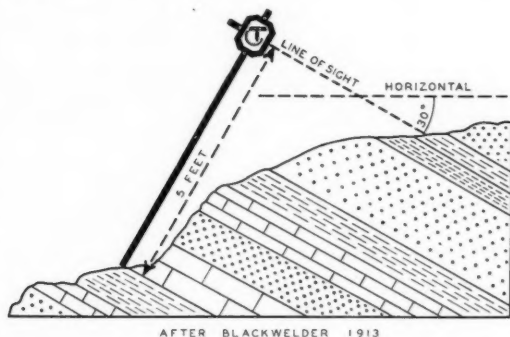


Fig. 3.—Diagram illustrating the use of the Jacob staff in measuring inclined strata.

The practicability and reliability of the hoe-handle method was proved by Payne. He measured a section aggregating several thousand feet in thickness. The section was checked by map calculations. Later, the same section was measured by the transit and the percent of error of the hoe-handle method was determined to be low.

A treatment of all the methods for determining the true thicknesses of strata is beyond the scope of this paper, although the topic is fundamental to the correct stratigraphic allocation of specimens and therefore to various types of interpretations. Careful work is as valuable for theoretical or interpretive geology and paleontology as for economic geology. For the sake of required accuracy, sections are measured and sampled where the geologic structure is as simple as possible. Hence, the determinations of thicknesses of members

<sup>6</sup> Letter dated July 30, 1941.



and formations as a rule are not difficult, provided, among other things, that the outcrops are continuous enough to preclude the possibility of faulting or great change in dip of strata within the section under consideration.

Three fundamental corrections are necessary in computing true thicknesses of inclined strata: (1) correction for the direction of the section; i.e., the angle of the section to the strike of the beds; (2) correction for the angle of the section to the horizontal; e. g., angle of the creek bottom or slope to the dip of the strata; and (3) correction for the dip of the strata.

These corrections can be made rapidly in the field as the section is being measured. The first correction, involving apparent dips in a section measured not normal to the strike of the strata, can be solved with an "apparent dip protractor" described by W. S. T. Smith (1925). The other two corrections can be solved graphically with the aid of a special protractor which has been designed by Mason Hill (1942). References to other methods of computing thicknesses are given in the selected bibliographic references.

*Labelling of samples.*—Each sample must be labelled well enough so that its exact location can be easily determined. The first essential is to give the sample a legible identifying number. This number is recorded on the map on the side of the symbol which denotes the exact point where the sample was collected, except where closely spaced samples make this unfeasible. The number and its location also are recorded in a notebook, and when samples are too closely grouped to be plotted on the map their locations with respect to plotted samples are given in the notebook.

The use of consecutive serial numbers has many variations. One geologist may number his localities consecutively throughout the year, no matter where he makes his collections. He will place the last two numbers of the particular year before the locality number; thus "2944" means his locality number 44 in the year 1929. Another geologist places the initial of his surname before each number; thus, "S-185" means Smith's locality 185. The California Academy of Sciences writes all localities as "C.A.S. 42," Stanford University employs the initials, "L.S.J.U." and so on. A collector connected with an organization maintaining a permanent register of localities may assign himself locality numbers before going into the field. Whatever the system, the serial number is placed upon the sample container in the field at the time of collection.

Long field experience has convinced W. S. Adkins<sup>7</sup> that the following system is a satisfactory one. If a person is planning work in a certain area, say in California or Texas, he can adopt a permanent labelling system. He has a locality book, preferably bound, in the office. He may have a Texas locality book, a California locality book, and an Oklahoma locality book. The name of the state need not be designated on the sample container, but the county

<sup>7</sup> Written comment by W. S. Adkins, February 24, 1941.

(or division of the state) will be designated by a symbol. The following are examples:

Tr-1-Au—Travis county (Texas), locality 1 of that county; Austin Chalk. (Detailed description is recorded in locality book.)

NL-1-Au—Nuevo Leon (no county), locality 1 in that state; Austin chalk.

CO-110-Au—Coahuila, locality 110 in that state; Austin chalk.

As a precaution it is well to duplicate the above symbols on a paper which is then folded and placed inside the sack. On the outside of the cloth sack Adkins writes the symbols and numbers with an old style indelible pencil. Care should be taken to avoid pencils which smear or run.

R. Wright Barker has used a similar system of labelling bags in his field work. In commenting upon a preliminary draft of this paper he pointed out that in many tropical countries it may take some days, even weeks, for the samples to reach the head office, and that because of this delay and the excessive humidity they may suffer from the destructive effects of mold and rot.<sup>8</sup> For this reason it is desirable, when possible, to dry the samples and to use a type of labelling that will not rot. R. M. Kleinpell recommends (personal communication) the use of aluminum tags which comprise detachable sections of a coiled aluminum tape. The tags have serial numbers stamped upon them and are detached and placed in a canvas bag, while corresponding locality descriptions are recorded in the field notebook. Others who have worked in the tropics poison their labels by washing them in a weak solution of corrosive sublimate to prevent their being destroyed by mites and insects.

The system of labelling should be simple and accurate, no matter what its details may be. Usually the serial number is supplemented by a brief indication of the area. Much valuable time can be wasted in the field by writing duplicate details in both a field book and on the labels. Thus, stratigraphers adopt a numbering system which reduces to a minimum the time necessary for writing adequate field labels and for recording the localities in the field notebook. Enough has been said about the numbering system to indicate that it is largely based on personal choice and experience in a given region. The main requisites are simplicity, conciseness without sacrificing completeness, and consistency.

*Geographic location.*—Figure 4 explains several methods of determining the geographic location of samples. Also shown in the illustration are forms for field labels which may be stamped on the bags or enclosed in them. These field labels contain space for more information than is needed, although it is always necessary that such a record of location be written in the field notebook or locality register book. The label provided with the lot number blank is the type used by several oil companies.

<sup>8</sup> Carrol Lane Fenton reports that he has folded good bond paper in heavily waxed paper when samples were moist.

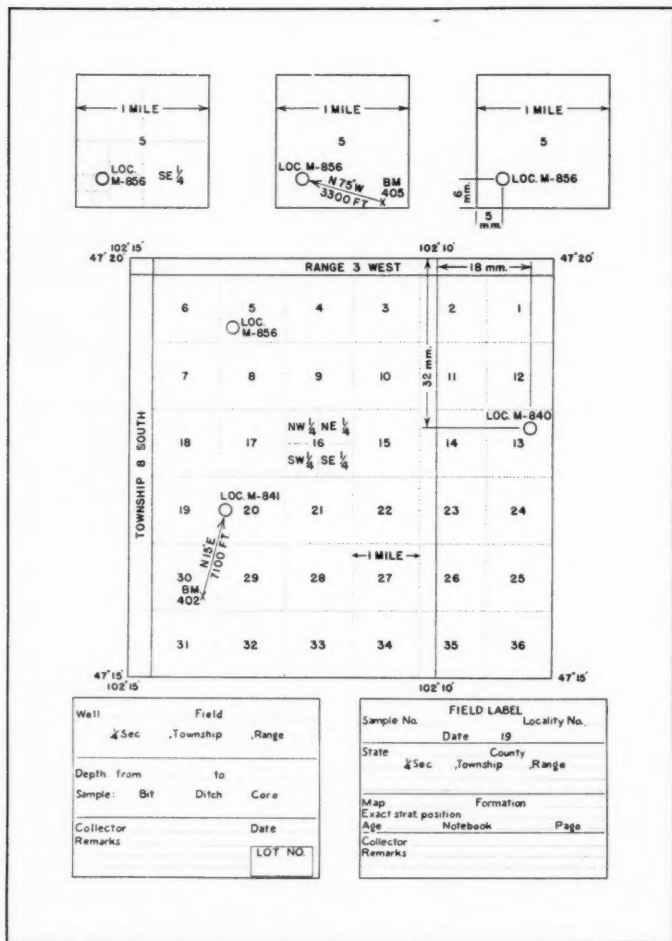


Fig. 4.—Map of a township (center), individual sections (top), and two field labels (bottom). Each section is one square mile. Three methods of indicating the location of Locality M-856 are given in the upper enlarged views of Section 5.

Both field labels of the kind illustrated and permanent records should contain a reference to some map. One should always bear in mind that the purposes of a locality description are several, among which two are most important: (1) to permit the plotting of the localities on a regional map, and (2) to assist another collector in finding the locality in order to obtain additional specimens.

It is simple to record the geographic occurrence of fossils in those regions which are "sectionized." Figure 4 illustrates how locations may be made in such a region. The enlargements of Section 5 in the upper part of the figure show three ways of locating Locality M-856. Other examples follow.

A written description of Locality M-856 would read: Lompoc quadrangle, 1000 feet north, 1000 feet east of the southwest corner of Section 5, Township 8 South, Range 3 West, Mt. Diablo Baseline and Meridian. In abbreviated form this becomes Lompoc quad., 1000 ft. N., 1000 ft. E., SW cor. Sec. 5, T. 8 S., R 3 W., M. D. B. and M. This requires little space and is accurate. Further details of local physical features should be recorded in the permanent record for the locality, but those details are omitted here.

Another concise method of geographic placement where topographic maps are available is to give measurements scaled off in millimeters from the intersection of a parallel of latitude and a meridian of longitude, as shown in Figure 4, locality M-840 in the northeast quarter of Section 13. This locality scaled off on the original base map is 18 mm. east of meridian  $102^{\circ} 10'$ , and 32 mm. south of latitude  $47^{\circ} 20'$ .

Another method, particularly useful where the map bears few or no points of reference, is to describe the locality by two angles formed between lines drawn from the locality to the bottom left and right hand corners of the map and the bottom edge of the map. Locality M-856 in Figure 4 could, for example, be described as  $77^{\circ}$ ,  $48^{\circ}$  where these angles are given for the left and right hand corners, respectively. This system is particularly adaptable to airplane photographs and can be used on such photographs as the worker might take in the field. One advantage is that it can be used on maps or photographs where scale has been altered by enlargement.

Another method is to record the azimuth and distance from a permanent monument, such as a benchmark. Note Locality M-841 in Figure 4, Section 20. This locality is 7100 feet North  $15^{\circ}$  East of B. M. 402.

The recording of latitude and longitude is, in addition to other data, particularly useful in little known regions or when a hydrographic chart is used as the base map.

*Stratigraphic position.*—One should record the stratigraphic position of a sample as well as its geographic location. The geologic map, Figure 5, shows an area of massive igneous rocks (granites) unconformably overlain by formation "A" which, in turn, is succeeded by formation "B," the younger of the two. Both formations dip toward the east. Each formation consists of several

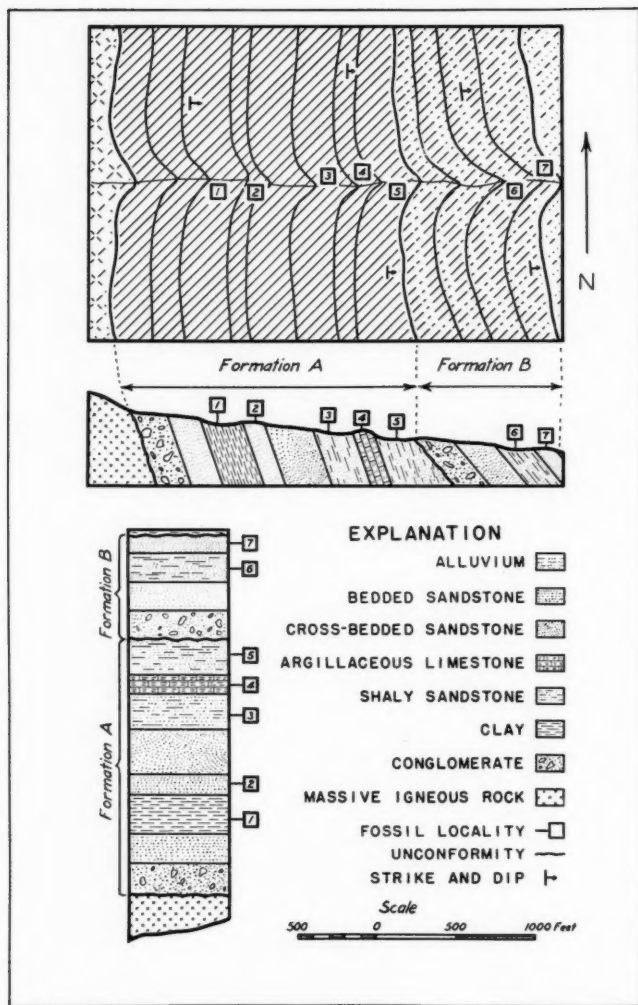


Fig. 5.—Hypothetical geologic map, cross-section, and columnar section illustrating one method of plotting collecting stations. The center of each square on the map (upper figure) is the exact spot of the sample. In the middle and lower figures the exact stratigraphic placement of the fossiliferous stratum is shown by the lines from the squares to the sections.

members; each member has been mapped across the area. The limits of these members are shown on the map by full lines. The basal member of formation "A" is a conglomerate; the second member is a well-bedded sandstone, and so on. These members were differentiated on the basis of lithology aided by the usual criteria employed in mapping, such as topographic expression and the color of the outcrops.

In addition to labelling the uppermost sample shown in formation "A" on the geologic map (Sample No. 5), its geographic location and the fact that it was collected from a shaly sandstone 100 feet below the top of formation "A" are written on the sample bag and in the field notebook.

*Plotting localities on the map.*—The location of a sample is plotted on a map for the express purpose of showing its exact geographic location and also its stratigraphic position in case a geologic map is used. Whether the symbol denoting the position of the locality in a cross, triangle, square (as in Figure 5), or some other symbol is unessential. It is essential that this symbol be plotted on the map at the exact point at which the sample was collected.

*Plotting localities on cross sections.*—The positions of collecting localities are indicated on geologic cross sections as well as on maps, as in the section below the map in Figure 5. Note that locality 1 is in member 3 of Formation "A," locality 2 is in well-bedded sandstone, and so on. The line indicating each locality is drawn from the precise horizon at which the fossils were collected.

*Plotting localities in geologic columns.*—The third type of allocation of specimens is shown in the geologic column at the bottom of Figure 5. Here the strata are delineated as they must have been laid down originally. The exact position of each collection station in the section is shown at the precise level where the collection was made, not only the position in the formation but also the position within the individual member. Fossils at locality 1, for example, occur 500 feet stratigraphically above the igneous rocks at the base of the section. Locality 2 is 220 feet above locality 1, and so on. Such a column is not unlike many well records and the principle is the same.

The number sign used in this column is a customary convention in some organizations. Other companies use a modified scheme. Many workers prefer to place the numbers of the localities in the graphic column itself. All systems have the same purpose: to show the precise stratigraphic allocation of the collection.

*Transportation of specimens from field to laboratory.*—Care should be taken that the sample containers can be placed in burlap sacks at the site of the collection. If the samples are to be subjected to rough handling, they should be transferred from the gunny sacks at the shipping point and placed in durable containers, such as wooden boxes. Invoices should always accompany shipments from the collector to the laboratory; an itemized list of samples, in triplicate, is sometimes required.

### Collecting Well Samples

*Importance of subsurface samples.*—The petroleum paleontologist or geologist is generally more concerned with the correlations of strata based upon subsurface than upon surface samples. In view of the value of well cores and cuttings, and because wells cannot be sampled time and time again like a surface section, it is imperative that great care be exercised in collecting subsurface samples. Special precautions should be taken against the possibility of contamination of samples and to secure the proper and legible labelling of them.

The following is an example of an error in correlation caused by the improper labelling of samples. Some time ago a paleontologist reported the presence of a certain faunule from a well drilled in the San Joaquin Valley, California. Other paleontologists who had access to the cores of the well had expressed the opinion that the drill was stopped short of the strata containing that faunule. Investigation proved that the collector who had reported the faunule had mixed the samples of two different wells, in one of which the characteristic faunule did occur and in the other of which the faunule was absent. It is conceivable that such an error, if not discovered in time, might result in the abandonment of a well before reaching a possible oil sand. In this particular case the discovery was made possible by the fact that several other geologists had samples from both wells, and their core samples had been carefully stored as records. Had the material not been kept, the error could not have been detected as the well was abandoned. A surface section could have been resampled. The collection of microfossils from subsurface sections places a premium upon the care and understanding of the sampler.

*Core tray tags.*—A core, on being taken from the core barrel is placed in enough three feet long, galvanized iron, core trays to accommodate the entire length of the core. Then to each tray is wired a tag on which is written the upper and lower depths of the interval cored, the number of the tray, and the length of core recovered. Figure 6 is an example of such a tray tag. The end of the tray containing the lowest segment of the core is the end generally labelled. The trays are numbered consecutively, but tray no. 1 may contain either the top or the bottom of the core, depending upon the system of numbering followed by the operator. Therefore, one should make certain which system is used in the particular well being sampled, asking the driller when in doubt.

*Contamination.*—Particular care should be exercised to prevent contamination. Occasionally, one will note the presence of a few fragments of shale or sandstone at the top of the core, while the remainder of the core may be comparatively well preserved. Sometimes the lithology of these fragments is so different from that of the rest of the core that one can identify them readily as being cuttings or cavings which have settled to the bottom of the hole and have been picked up in the core barrel. One should avoid taking a sample where the core is composed of drilling mud studded with shale fragments.



Also, before sampling a core, one should peel off the crust of rotary drilling mud which often forms a sheath around it. This further avoids contamination. In crowded core houses where many trays of cores are stacked on shelves, one above the other, material from the upper shelves may fall and become mixed with material on the lower shelves. Such mixing is sometimes obvious. In a string of cores of monotonously similar, crumbly shales, however, shale fragments dropped from a higher to a lower tray might be difficult to detect. If there is reason to believe that such may be the case, one should brush aside the upper layer of the shales and take a sample from the undisturbed part of the core. If any doubt remains concerning the possibility of contamination, a note to that effect should be written on the sample bag.

*Amount of sampling.*—Some companies may be interested only in certain parts of a well and will have samples collected at certain critical places in the section. In such cases the exact position of the sample is estimated within the cored interval. If the recovery of the core is poor, the accuracy of such an estimate will vary according to the number of feet of difference between the cored interval and the amount of core recovered.

A diagram of a core tray tag, which is a rectangular card with a pointed top. At the top center is a circular hole. The tag contains several lines of text for data entry, each followed by a horizontal line for writing. The text includes: DATE, COMPANY, WELL NO, DRILLER, CORE NO, FROM TO, NUMBER OF TRAYS USED, THIS END IS BOTTOM OF TRAY NO, REMARKS, and TRAY NO 1 IS TOP OF CORE PLACE TAG AT BOTTOM END OF TRAY. To the right of the tag is a vertical double-headed arrow labeled 120 MM. Below the tag is a horizontal double-headed arrow labeled 60 MM.

DATE \_\_\_\_\_

COMPANY \_\_\_\_\_

WELL NO \_\_\_\_\_

DRILLER \_\_\_\_\_

CORE NO \_\_\_\_\_

FROM \_\_\_\_\_ TO \_\_\_\_\_

NUMBER OF TRAYS USED \_\_\_\_\_

THIS END IS BOTTOM OF TRAY NO \_\_\_\_\_

REMARKS \_\_\_\_\_

\_\_\_\_\_

\_\_\_\_\_

\_\_\_\_\_

\_\_\_\_\_

TRAY NO 1 IS TOP OF CORE  
PLACE TAG AT BOTTOM END OF TRAY

120 MM

60 MM

Fig. 6.—Core tray tag.

Other companies require their collectors to sample every tray. When this is done the number of the core, the interval cored, the number of the tray, total number of trays in the core, dominant lithologic type (sandstone, conglomerate, shale, limestone, etc.), presence of fossils, and number of feet of core in each tray may be indicated on the sample bag on which the name and location of the well have been previously stamped.

*Bags and labels.*—The label shown in the lower left of Figure 4 is a common form printed on a sample bag used for well samples. Many variations of this form are in use today, but nearly all of them include the essential data indicated. Parts of the form can be filled in with a rubber stamp in the laboratory in order to speed up the sampling at the well. For instance, the lot number, well name, field, location, collector, and date will be the same for all samples from one well. The depths, lithologic and paleontologic remarks, kinds of sample (ditch, bit, or core) can be filled in only as the samples are collected at the well. The samples from a single well are frequently numbered consecutively as an aid in arranging the samples for ready filing.

The information given on sample bags is generally the minimum necessary for proper identification. Many California operators consider that the minimum data to be placed on the bag are four: (1) the name of the well; (2) a brief indication of the location of the well, or in lieu of that the lot number for all the samples from the well; (3) the depth of the sample; and (4) whether the sample is a core, ditch, or bit sample. All operators, in California and elsewhere, insist that the information written or printed on the sample bag be legible and preferably permanent.

*Description of well cores.*—Lithologic descriptions of well cores are a valuable aid in making correlations with other well and outcrop sections. In the event that one has the opportunity to describe the lithology of the subsurface samples as well as to collect the material, it is well to make the lithologic descriptions first and take the samples later. By so doing it is possible to see the relationship of the various formations and to note the most fossiliferous portions of the section. Also, such preliminary descriptions aid in the detection of possible contamination of cores and in choosing the most likely places to sample if it is not required that samples be taken at some fixed interval.

As complete a megascopic examination of the cores as possible should be made, in which special attention is devoted to the description of possible "marker" beds, such as bentonite, glauconitic sandstone and shale, ash beds, chert, or any distinctive bed. The strata above and below formational contacts should be carefully described. With the aid of a hand lens the presence of microfossils, larger invertebrates, unusual minerals, degree of sorting, and other features can be noted. A statement regarding the presence of oil, if any, the degree of saturation, presence of chloroform or acetone oil cuts and their colors, and even the odors of the shales and sandstones should be given.

The recording of such data should follow some uniform scheme. The core description given in Figure 7 is one form commonly used. The heading of the

SAMPLE CORE DESCRIPTION				
<p>OPERATING COMPANY</p> <p>LEASE NAME AND WELL NUMBER HURON AREA, FRESNO COUNTY, CALIF. LOCATION: 2400' N., 1900' E., S.W. CORNER SECTION 8, T. 20 S., R. 17 E., M.D.B. &amp; M. ELEVATION: 234' (DERRICK FLOOR) CORE DESCRIPTION BY J. J. DOE</p> <p>7810' TOP KREYENHAGEN (ELECTRIC LOG) 8813' TOP DOMENGINE (CORED) 8827' BASE DOMENGINE (CORED) 8940' TOTAL DEPTH</p>				
CORE NO.	DEPTH FEET	THICKNESS	RECOVERY	DESCRIPTION
10	8804-8812	9'	9' 1'	(UPPER CORES OMITTED) <u>SHALE</u> , BROWN, HARD, PLATY, DIP 10°, FISH REMAINS. 5' <u>SAND</u> , GREEN-GRAY AT TOP TO GREEN AT BASE, FINE-GRAINED, WELL SORTED, TIGHT, <u>VERY GLAUCONITIC</u> , NO CUTS. 2' <u>SHALE</u> , BROWN TO DULL GRAY, HARD. 1' <u>SAND</u> , AS ABOVE, <u>VERY GLAUCONITIC</u> , PYRITE COMMON.  BASE KREYENHAGEN - TOP DOMENGINE, 8813'
11	8813-8822	9'	9'	<u>SAND</u> , LIGHT GRAY, WITH SLIGHT GREEN AND TAN CASTS, VERY FINE-GRAINED AND SILTY, TIGHT, <u>GLAUCONITIC</u> , FAINT PETROLEUM ODOR AND FAINT CCL <sub>4</sub> CUTS, RARE SHELL FRAGMENTS.
12	8822-8829	7'	6' 1'	<u>SILTSTONE</u> , DARK GRAY, SANDY, ANGULAR QUARTZ GRAINS, <u>GLAUCONITIC</u> , ABUNDANT FRAGMENTS OF OSTREA IDRIAENSIS (?), AND TWO CASTS OF GLYCIMERIS SP., COMMON LARGE ROBULUS-LIKE FORAMINIFERA. 5' <u>SILTSTONE</u> , DARK GREEN-GRAY, VERY SANDY AND COARSE GRITTY WITH FEW BLACK GRANULES AND SMALL QUARTZ PEBBLES, <u>GLAUCONITE</u> AND SHELL FRAGMENTS COMMON.  BASE DOMENGINE, 8829' (LOWER CORES OMITTED)

Fig. 7.—Hypothetical core description as written by one collector in California. The format is similar to that used by many oil companies in that area.

core description contains the name of the operating company, lease name or number, well number, section, township, range, and the describer's name. Below the heading is given the depths of the formational contacts, marker beds, and total depth of the well. In parenthesis after the names of formations or marker beds it is indicated whether points were picked in cored intervals, from ditch samples, or from an electrical log. Below this statement comes a tabulation giving the core number, the depth in feet of the core, the number of feet cored, and the number of feet of rock taken out of the core barrel. The final column bears the lithologic description of the core samples. In this description the dominant rock type is stated first, followed by the color, texture, hardness, and additional remarks, such as mineralogical and paleontological content, oil cuts, and dips. When such a description is typed in the office it is a widespread practice to add the drilling and production history of the well from the date of spudding to the date of completion or abandonment. Attached to the record may be the driller's log or an electric log in order that the description of the uncored intervals may be completed.

When the time available for describing the core samples from a given well is too limited for a detailed core-by-core examination, one may have to be content with noting the dominant lithologic types and the position of formational contacts and marker beds.

*Ditch samples.*<sup>9</sup>—Although the best available method of getting information concerning formations encountered in drilling wells is by taking core samples, this method has the disadvantage of being expensive. No more cores are taken, therefore, than is absolutely necessary. Information as to the uncured intervals is pieced together by electrical logs and by the systematic collection of cuttings brought up from the bottom of the hole by the circulation of drilling fluid. These cuttings are called ditch samples. A study of them shows not only the general lithology of the formations but also their paleontologic content. The limitations which must be kept in mind in using ditch samples are explained below.

Consideration of methods used in collecting rotary drill cuttings should be prefaced by a statement of what constitutes cuttings. Part of the drilling is done by the bit and part of the material is forced from the bottom of the hole by the force of the mud flow. Another source of material is the side walls cut by the reamers. Some of these fragments reach the surface of the ground as pieces an inch or more in length. Some of the other material, such as sand and silt, is broken into its component particles and some of the clay is dissolved in the mud. Therefore, rotary cuttings in the broader sense are the sum total of fragments dislodged from the bottom of the hole by the grinding action of the bit and the hydraulic force of the mud stream. More of the clay breaks up in the light, watery mud that is occasionally used in the upper part of the wells than in the heavy, viscous mud used at greater depths. Rotary cuttings, there-

<sup>9</sup> For aid in the preparation of this section we are especially indebted to S. W. Lowman.

fore, reach the surface in all stages of disintegration, and one cannot safely exclude the minute particles from the consideration of the cuttings collection because of the possible microfaunal content of the softer horizon.

Several methods of collecting ditch samples are in common use, but they may be classified into two main groups: (1) settling and (2) sieving methods. The settling method, of which many variations exist, consists of diverting a small part of the drilling fluid into a small settling box immediately after it issues from the well. Part of the cuttings settle out in this box and are collected at regular intervals. "Box" methods can be used effectively in areas where the strata are sufficiently indurated to produce cuttings that settle from the drilling fluid when the rate of flow of the fluid is sufficiently checked. The prime requisite of "box" sampling is that the ratio of the size of the settling trough to the amount of mud is such that the rate of flow of the mud will be slowed sufficiently to permit the cuttings to settle. This ratio is affected by the weight and viscosity of the mud and the degree of induration of the cuttings. Heavy, viscous mud will support cuttings at a slower rate of flow than will a light, thin mud. When drilling conditions permit, a fraction of the highly viscous mud should be thinned with water in the sampling box or in the bypass mud line flowing into the box. The size of the box should be related to the size of the samples desired. Relatively large volumes of mud must be sampled in order to obtain large amounts of material and this, in turn, necessitates a larger box in which to check the flow. Under usual conditions, a box five feet long and one foot wide is sufficient for ordinary needs. For further information the reader is referred to the descriptions by Clark, Daniel, and Richards (1928). The centrifuge sand separator has possibilities, but it is not in general use.

The greater proportion of rotary cuttings are now collected by some modification of the second—"sieving" or "straining"—method. Most rigs are now equipped with a mechanical vibrating mud screen or "shaker" which removes the fragments of cuttings from the mud stream by passing the mud as it leaves the well through a rapidly vibrating screen of about 20 mesh to the inch. The purpose of this screen is to clean the cuttings from the drilling fluid as it issues from the well. The screen is set up at a slight angle from the horizontal so that after the mud passes through it the cuttings are shaken down to the lower end of the screen, where they fall into a trough. They are collected from this trough at regular intervals, and, after each collection is made, the trough is cleaned in readiness for the next sample.

Some portion of the fine material which remains on the shaker screen generally adheres to muddy clay fragments. It is common practice on the Gulf Coast and in most other areas to remove this fine material from the sample by rinsing the coarser fragments before drying, sacking, and shipping them to the laboratory. It has been thought that this is necessary in order to remove the loose sand which greatly impedes the study of the samples after they have

been washed for paleontologic examination. Recently, however, H. V. Howe (1941) announced that effective separations of foraminifers from the sand can be made by the use of soap as a flotation agent. It seems advisable, particularly in a new area or in the reexamination of an old area, that near total samples of rotary cuttings should be collected and the washed residues treated by the soap flotation process.

More nearly total samples of cuttings can be collected on a non-vibrating screen than on the usual shaker. This requires constant attention to prevent clogging and it is consequently an expensive method of collecting. Hence, it is used only in the collection of samples to be used in basic, rather than routine, investigation. M. A. Hanna has employed another method for collecting near total samples. This consists of a double cheesecloth sack through which the drilling mud drains, leaving behind it all except the finest particles. When the sack is full to overflowing, it is set aside to drain and is replaced by another sack. In routine work it is advisable to use those guide fossils which are ordinarily found in the more indurated formations, because most sets of rotary cuttings which will be available for examination will be rinsed shale shaker cuttings.

Shipment of cuttings from the well to the laboratory is generally made in cloth sacks, the depth and the well name being written with indelible pencil on a tag sewn into the side of the sample bag. The samples should be dried before shipment in order to keep wet mud from passing through the sack on to the tag and rendering the label illegible. In some humid areas ovens are needed to dry the samples, especially where speed is required in the transmission of samples from the field to the laboratory. A somewhat more expensive method involves the use of cans for cuttings; this avoids the necessity of drying the material before shipping and greatly speeds the transmission of samples from the field to the laboratory.

The interval at which ditch samples are collected differs with conditions. They may be taken at 10-foot intervals, at drilling breaks (lithologic changes), or they may be taken when a particular "zone" or formation is expected. Under some conditions samples may be collected at 10-foot intervals throughout the whole depth of the well, while in many instances only at such an interval for short distances where lithologic and paleontologic markers are expected to occur. S. W. Lowman has the following to say concerning the interval for collection:

The interval at which cuttings are collected in the upper part of the well should be calibrated to the speed of drilling and thereby to the capacity of the roughneck. If he is requested to collect two or three samples a joint while drilling is progressing at 1000 feet or more a day, he will probably make one sample do for three. Having started this practice in the upper part of the well he may continue even in portions where the drilling progress is sufficiently slow to permit collection of three samples to a joint. We have found it desirable to hold our requests to a 30-foot interval during fast drilling (surface to 3000 or 6000 feet depending on the area), and to a 10 or 15 foot interval from there on down.

The depth from which ditch samples are logged is almost never the true depth from which they actually came, even if contamination by caving is disregarded. The reason for this discrepancy is that it takes a considerable time for the cuttings to travel from the bottom of the hole up to the top where they are collected. During this time the bit continues to cut downward and by the time the cuttings reach the surface and are collected, the bottom of the hole is below the stratum from which they came. By way of illustration let us suppose that a well is being drilled in a soft formation at the rate of one foot per minute. The depth is such that it takes fifteen minutes for the cuttings to travel up from the bottom. The ditch samples that are collected will be labelled with the depth of the bit at the time of collection, and in order to find the true depth it will be necessary to subtract fifteen feet from the depth as logged. The main factors which control this correction for lag are the depth and diameter of the hole, the outside diameter of the drill pipe, the drilling speed, and the output of the mud pumps which circulate the drilling fluid.

Where the drilling progress is rapid at great depth, the correction for lag is considerable, but where the depth is shallow this correction is so small as to be negligible. For those wishing further information, reference may be made to the publications by Clark, Daniels, and Richards (1928), Kraus (1924), Suman (1922), and Uren (1934).

Despite the fact that the cuttings in an individual sample may have come from several different strata, ditch samples are of value in picking "tops"—the upper stratigraphic occurrences of characteristic species of fossils or of distinctive rock layers. For example, suppose that the ditch samples from a well between the depths of 3000 and 4000 feet yield a Pliocene microfauna; from 4000 to 5000 feet a Miocene fauna as well as a few Pliocene species; and the interval from 5000 to 6000 feet carries an Oligocene assemblage together with some Miocene forms and even a number of Pliocene species. The assumption would be that the strata from 3000 to 4000 feet are Pliocene, that the first Miocene beds were encountered at 4000 feet and extended down to 5000 feet, and that the rocks from 5000 to 6000 feet are Oligocene in age.

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## Age of the Martinez Formation of Pacheco Syncline, Contra Costa County, California\*

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An excellent section of Eocene strata is exposed on the southwest limb of Pacheco syncline, south of the town of Martinez, California. The lower Eocene beds there represent the type Martinez formation, a name proposed by J. D. Whitney, in Gabb, 1869, p. xiii, (see bibliography). The line of section discussed in the present report runs through Muir Station on the Santa Fe Railway, parallel to and one mile distant from Gabb's (1865, p. 14) section. The exact locality is shown on the United States Geological Survey map of the Concord Quadrangle, and on the accompanying map, Figure 1. The purpose of this report is to present evidence to prove that the upper part of the type Martinez formation is of middle Eocene age.

The species found in the strata on the southwest limb of the Pacheco syncline are recorded on the accompanying columnar section (Figure 2).

### FORMATION NAMES

The Eocene section of the Pacheco syncline is a conformable sequence of strata measuring  $5400 \pm$  feet in thickness. These strata were mapped as two formations, Martinez and Tejon, by Merriam (1897), Dickerson (1914), Lawson (1914), and Weaver (in Tolman, 1932). The name Tejon was applied to the upper 2800 feet of the Eocene beds on the basis of supposed equivalence in age rather than on similarity in lithology to the type Tejon formation of Kern County, California. Since exact contemporaneity is difficult to prove, and since these strata are such a great distance from the type Tejon and can not be traced into them, another formational name might be advisable, or the term Markley used instead. However, until further information is available, the strata in question are here called "Tejon".

### LOWER MARTINEZ FORMATION

The lower 2600 feet of Eocene beds at Pacheco syncline, mapped as the Martinez formation, represent a distinct cartographic unit. The lowest Eocene beds exposed are glauconitic sands which contain, at locality 2237, a Paleocene molluscan assemblage such as has been considered typical of the "Martinez Stage" throughout California. These lowermost Martinez strata rest with probable unconformity on beds mapped as "Chico," Cretaceous. No positive physical evidence of unconformity was found, but the foraminiferal faunule at

\* Editorial note. See the paper on "Collecting Microfossils" by Hubert G. Schenck and Robert T. White, *Amer. Midl. Nat.* vol. 28, no. 2, pp. 424-450, 1942. This paper is offered as an example of the results achieved by detailed collecting in a difficult area, as well as a contribution to West Coast biostratigraphy.



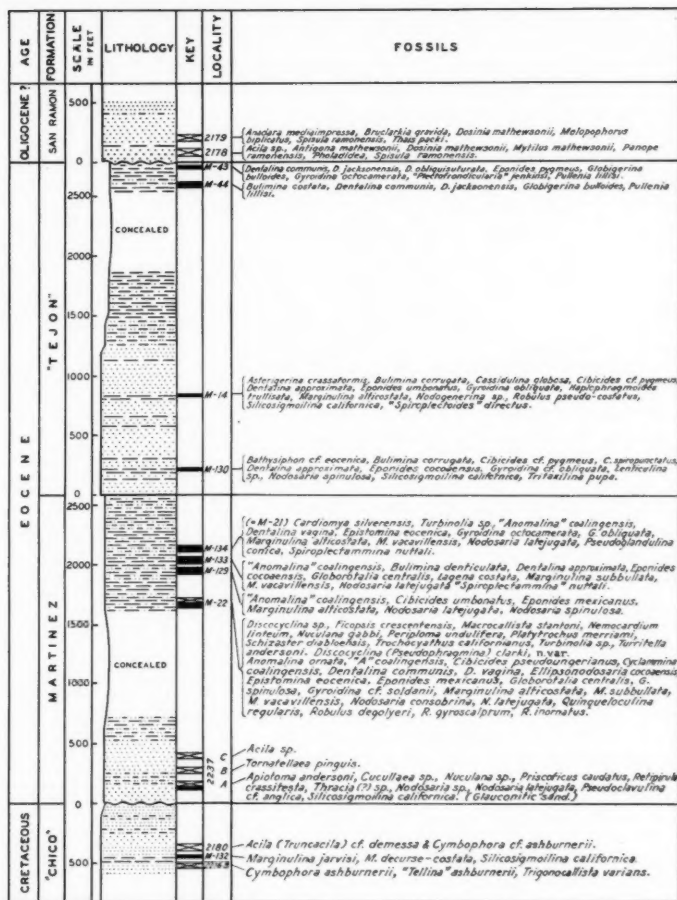


Fig. 2.—Stratigraphic section measured on the southwest flank of the Pacheco syncline, Contra Costa County, California. The symbols in the column headed Key show the exact strata from which fossils were collected. Solid black symbols refer to faunules composed of microfossils; the symbols with crossing diagonal lines refer to faunules composed of megafossils. The localities, numbered in the next column to the right, are recorded and described in the Register of Localities of Leland Stanford Junior University, and at the end of this paper.

*Marginulina jonesi* Cushman and Church, 1929, is a homonym of *Marginulina jonesi* Reuss, 1863, from the Lower Cretaceous of Europe. For the California species, Thalman (Eclage geologicae Helvetiae, vol. 30, no. 2, December, 1937—January, 1938—p. 348) proposed the name *decurse-costata*. In accordance with the rules of nomenclature, and because of a generic transfer proposed by that author, this species should now be cited as *Marginulinopsis decurse-costata* (Thalman), if workers accept the biological validity of the genus *Marginulinopsis* Silvestri, 1904.

Between the horizon marked by locality M-22 and the top of the Martinez formation as mapped are fossiliferous strata corresponding in age with beds commonly referred to as middle Eocene. For example, at locality M-134 there is a sequence of faunules similar to assemblages from the Arroyo Hondo shale on the west side of the San Joaquin Valley north of Coalinga. A faunule 500 feet above the *Discocyclus*-bearing beds at locality M-22 is said by B. L. Clark (oral communication) to be referable to his "Domengine Stage". Paleontologists are all agreed, therefore, that the beds between locality M-22 and the base of the "Tejon" formation as mapped are younger than the Clark and Vokes "Capay Stage", hence younger than Paleocene.

#### "TEJON" FORMATION

Conformable on the Martinez with an apparent gradational contact is the "Tejon" formation. The lower 1500 feet of this formation are composed predominantly of a light colored, medium-coarse-grained, micaceous sandstone with occasional intercolated thin layers of dark gray shale. These shales carry foraminiferal faunules (localities M-130 and M-14) that probably fall in the "Tejon and Transition Stage" of Clark and Vokes (1936). The faunules found at these two localities are considered to be equivalent in age to the Canoa silt (basal Kreyenhagen), of Kings County, California, and to the Nortonville shale of Contra Costa County, California. Ferguson agrees with these correlations, and adds that there is also a similarity to faunas found in siltstones which can be traced into lower type Tejon sands in Kern County, California.

The upper part of the "Tejon" formation is composed chiefly of siltstone and shale and the beds at the top of the formation (localities M-43 and M-44) carry a good foraminiferal assemblage. Some species found at these localities are listed below:

- M-43 *Eponides pygma* Hantken, in Church, 1931.  
*Nodogenerina bradyi* Cushman, in Church, 1931.  
"Planularia" *markleyana* Church.  
*Plectofrondicularia jenkinsi* Church.  
*Pullenia lillisi* Church.
- M-44 *Bulimina corrugata* Cushman & Siegfus.  
*Globigerina bulloides* d'Orbigny.  
*Pullenia lillisi* Church.  
*Rotaliatina* sp.

This part of the section is thought to be equivalent in age to the Kreyenhagen formation as mapped by Taff (1935) on the north side of Mt. Diablo, in Contra Costa County, California.

#### SAN RAMON FORMATION

Overlying the "Tejon" formation with angular unconformity are the distinctive coarse sands of the San Ramon formation, of supposed Oligocene age.



## SUMMARY

In summary, there is exposed, in the Pacheco syncline, a conformable sequence of Eocene strata, about 5400 feet thick, ranging in age from Paleocene to late Eocene. The upper 1000 feet of the type Martinez formation, as mapped, are correlated with other California deposits of middle Eocene age.

## ACKNOWLEDGMENTS

I am indebted to Lois T. Martin, of Stanford University, for checking the foraminiferal identifications, and to Glenn C. Ferguson, of the Union Oil Company of California, and Boris Laiming, of The Texas Company, for their opinions concerning the stratigraphic position of the various faunules. In addition, H. G. Schenck and A. Myra Keen, of Stanford University, and B. L. Clark and Herdis Bentson, of the University of California, aided in the identification of the megafossils.

## REGISTER OF LOCALITIES

All localities are on the southwest limb of the Pacheco syncline, Contra Costa County, California, and are recorded in the Locality Registers of Leland Stanford Junior University. The measurements (in millimeters) refer to distances on the United States Geological Survey topographic map of the Concord Quadrangle.

- M-14 11.5 mm south and 55 mm west of the intersection of Latitude 38°00' with Longitude 122°05'. From a clay bed in the sandstone through which the Santa Fe tunnel passes. The sample came from the roadcut directly over the tunnel. "Tejon" formation. Coll: F. Putlitz.
- M-22 15 mm south and 55 mm east of the intersection of Latitude 38°00' with Longitude 122°10'. Creek bank approximately 175 feet northwest of Santa Fe railroad trestle. Martinez formation. (Same as U. C. Loc. A-1447).
- M-43 45.5 mm west and 5.5 mm south of intersection of Latitude 38°00' with Longitude 122°05'. Approximately 4000 feet N. 60° E. from Muir Station, in vertical beds; 140-150 feet from west end of roadcut. "Tejon" formation. Coll: P. Wilcken and E. Watson.
- M-44 Same roadcut as M-43, but extending westward, samples ranging from 17 to 70 feet below the "Tejon"—San Ramon contact. Coll: P. Wilcken and E. Watson.
- M-129 15 mm south and 58 mm west of intersection of Latitude 38°00' with Longitude 122°05'. In roadcut 165 feet S. 38° W. from Muir Station. Martinez formation. Coll: A. D. and E. A. Watson.
- M-130 13 mm south 56.5 mm west of intersection of Latitude 38°00' with Longitude 122°05'. Approximately 100 feet southwest of tunnel near Muir Station, in cut bank along railroad. "Tejon" formation. Coll: E. Watson.
- M-132 21 mm south and 75 mm west of intersection of Latitude 38°00' with Longitude 122°05'. Railroad cut west of tunnel above Franklin Canyon Inn. Opposite Santa Fe Railway marker P.S.C. 2°00. "Chico" formation, 490 feet below the top of the Cretaceous as exposed. Coll: A. D. and E. A. Watson.
- M-133 In roadcut 60 feet S. 15° E. from northwest corner of Muir Station; 14 mm south and 57 mm west of intersection of Latitude 38°00' with Longitude 122°05'. Martinez formation. Coll: A. D. and E. A. Watson.
- M-134 13 mm south and 56 mm west of intersection of Latitude 38°00' with Longitude 122°05'. Roadcut 150 feet east of northwest corner of Muir Station. Martinez formation. Coll: A. D. and E. A. Watson.

- 2178 45 mm west and 4.5 mm south of intersection of Latitude 38°00' with Longitude 122°05', or 3075 feet N. 56° W. from Muir Station. San Ramon formation. Coll: P. Wilcken and E. Watson.
- 2179 Same as 2178 but nearer east end of roadcut; 3210 feet N. 57° W. from Muir Station. San Ramon formation. Coll: P. Wilcken and E. Watson.
- 2180 75 mm west and 20 mm south of intersection of Latitude 38°00' with Longitude 122°05'. Railroad cut—500 feet west of Santa Fe Railway tunnel above Franklin Canyon Inn. "Chico" formation. Coll: A. D. and E. A. Watson.
- 2216-B 76.5 mm west and 18 mm south of intersection of Latitude 38°00' with Longitude 122°05', or approximately 3450 feet S. 80° W. from Muir Station. "Chico" formation. Coll: L. Martin and E. Watson.
- 2237 70 mm west and 16.5 mm south of intersection of Latitude 38°00' with Longitude 122°05'. Roadcut across from old John Muir homestead. Loc. 2237-A is approximately 225 feet S. 83° W. from southwest corner of bridge over Franklin Creek. Martinez formation. Coll: A. D. and E. A. Watson.

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## Foraminiferal Homonyms

Hans E. Thalmann

### PURPOSE

This note aims to draw the attention of workers to two categories of problems: (1) nomenclatural problems caused by the unstable classification of protists, and (2) the question whether names of varieties of animals are to be treated as coordinate with species and subspecies in consideration of primary and secondary homonyms.

In order to be concrete, several examples will be given so that the problems may be readily grasped. These examples have been chosen at random; they could be multiplied many times over. Examples will be cited for the nomenclatural problems caused by unstable classification of protists, and others will be given to clarify the problem of primary and secondary homonyms.

### NOMENCLATURE PROBLEMS CAUSED BY UNSTABLE CLASSIFICATION OF PROTISTS

Numerous organisms have been placed by some workers in the animal kingdom and by others the same organisms have been allocated to the plant kingdom. Article 1 of the "International Rules of Zoological Nomenclature" reads as follows:

Zoological nomenclature is independent of botanical nomenclature in the sense that the name of an animal is not to be rejected simply because it is identical with the name of a plant. If, however, an organism is transferred from the vegetable to the animal kingdom its botanical names are to be accepted in zoological nomenclature with their original botanical status; and if an organism is transferred from the animal to the vegetable kingdom its names retain their zoological status.

An example of this category of problems is the case of *Listerella*. Cushman (1933) first named the foraminiferal genus *Listerella*, with *Clavulina primaeva* Cushman, 1913, as the genotype by original designation. In 1906, however, Jahn had applied the name *Listerella* to a genus of myxomycetes. According to Neave (1939, p. 970), both genera of organisms are animals. Since this constitutes a transfer from the vegetable to the animal kingdom in the sense of Article 1 of the Rules, the botanical name is to be accepted in zoological nomenclature and *Listerella* Jahn antedates *Listerella* Cushman.

H. G. Schenck (personal communication) informed Cushman in a letter dated July 1, 1940, that his generic name is a primary homonym. Cushman in reply stated that the generic name *Martinottiella* Cushman, 1933, would then apply, *Listerella* Cushman being treated as a synonym. This biological opinion is not shared by the present writer. *Martinottiella* is a valid genus, genotype *Clavulina communis* d'Orbigny, 1846. It differs from *Listerella* Cush-

man because it skips the biserial stage of development which is prominent and typical in the genotype of *Listerella* Cushman. The genotype of *Martinottiella*, moreover, shows an abrupt change from the initial triserial arrangement of chambers to the uniserial stage and has a different aperture. These biologic units differ also in geologic record.

Since it is unlikely that dimorphism accounts for these morphological differences, the conclusion is reached that two distinct biologic categories are represented by these foraminifers. The name *Listerella* Cushman becomes a homonym on account of Neave's allocation of the genus *Listerella* Jahn from the vegetable to the animal kingdom. In order to avoid further confusion the following nomenclatural change is here made:

*Schenckiella* Thalmann, nom. nov., for *Listerella* Cushman, 1933, non Jahn, 1906. The genotype is *Clavulina primaeva* Cushman, 1913, U. S. Nat. Mus. Proc., vol. 44, No. 1973, p. 635, pl. 80, figs. 4, 5, from a depth of 476 fathoms, vicinity of Sibuko Bay, Borneo, Dutch East Indies. This genus is described by Cushman, 1933 and 1940 as follows:

"Test in early stages a trochoid spire with four or five chambers to a whorl, reducing later to three, then a series of two's, and in the adult uniserial; wall finely arenaceous; aperture terminal with a slender neck. Range: Eocene to Recent." Size: 0.80 to 4.00 mm.

It may be noted in connection with this problem that the genus *Listerella* Cushman was created before the transfer of *Listerella* Jahn from the vegetable to the animal kingdom. Some systematists might hold the viewpoint that the date of transfer should influence the nomenclatural decision and that *Listerella* Cushman had first claim upon validity in the animal kingdom. It is, however, the conviction of the writer that such a stand would create confusion.

Another example of nomenclatural problems caused by the unstable classification of unicellular organisms is the case of *Navicula*. A genus of the pelecypod family *Arcidae* was named *Navicula* by de Blainville in 1836. In 1822, however, Bory de Saint-Vincent had applied the name of *Navicula* to a diatom. At the time of the creation of the latter name, the diatom was regarded as an "animalcule"—an organism belonging to the animal kingdom. As Reinhart (1935, p. 17, footnote) and G. D. Hanna (1932, p. 120) have pointed out, this is a question which should be ruled on by the International Commission on Zoological Nomenclature. Does the generic name of the diatom preoccupy the generic name of the mollusk?

Unstable nomenclature is certain to result from shifting biological opinions. A considerable number of unicellular organisms have both a nutrition vacuole and a chromatophore, and thus belong to both the animal and plant kingdoms, to either one or to neither, according to the opinion of the biologist. Confusion will be lessened if taxonomists will follow the recommendation of the Commission on Zoological Nomenclature:

It is well to avoid introducing into zoology as generic names such as are in use in botany.

ARE NAMES OF VARIETIES TO BE TREATED AS COORDINATE WITH SPECIES  
AND SUBSPECIES IN CONSIDERATION OF PRIMARY AND  
SECONDARY HOMONYMS?

The question repeatedly arises whether a varietal name should be regarded as a primary homonym when the same name has already been in use for a species. The International Rules of Zoological Nomenclature at present apply the law of priority only to generic, subgeneric, specific and subspecific names. The Rules do not mention the classificatory units *variety*, *varietas*, *mutatio*, *forma*, and others, notwithstanding the fact that these units are widely used by many workers. As long as a variety, mutatio or forma is not elevated to specific rank no difficulties arise. The problem becomes evident, however, as soon as a variety is elevated to specific rank because of a shift in biological opinion. Indeed, it would seem that many systematists—micropaleontologists, entomologists, ichthyologists, and others—commonly regard varieties as a classificatory unit having at least subspecific rank in the sense of the Rules. Numerous examples might be given of foraminiferal varieties which have different stratigraphic and geographic ranges from the typical species. Enquiries addressed to several specialists elicited the opinion that the categories, variety and subspecies, commonly are used interchangeably; only the rare systematist differentiates between them.

Systematists generally recognize that specific homonyms fall into two categories: primary homonyms and secondary homonyms. A primary homonym is a specific name proposed in the identical name-combination of an earlier name, but representing a distinct biological unit. A secondary homonym is a specific name which, through generic reallocation subsequent to its proposal, becomes identical in form with an earlier name. The International Commission on Zoological Nomenclature should be appealed to for an opinion on the status not only of secondary homonyms among species and subspecies but also among varieties.

In the annual bibliographies and indices of the Foraminifera (Thalman, 1933 et seq.) attention has been called to all varietal names which are the same as previously-established specific names. This action will be continued unless the International Commission on Zoological Nomenclature renders an opinion to the effect that such varietal names are invalid.

Among the many primary homonyms in Foraminifera are the following: *Ammodiscus minutus* Dunn, 1942 → *A. abbreviatus* Cushman, 1910, var. *minutus* Ireland, 1939. (In this case *A. minutus* Dunn, 1942, is anyhow a homonym of *A. minutus* Paalzow, 1932.)

*Bolivina imbricata* Cushman, 1925, var. *inflata* Kleinpell, 1928 → *B. inflata* Heron-Allen and Earland, 1913.

*Bolivina subadvena* Cushman, 1926, var. *serrata* Natland, 1938 → *B. obsoleta* (Eley, 1859) var. *serrata* Wright, 1900. Natland's variety is at the same

time a secondary homonym of *Bolivina serrata* (Chapman, 1892), originally described as a *Textularia*, but later on shifted to the genus *Bolivina*.

*Listerella* (now *Schenckia*) *gracillima* Cushman and Bermudez, 1937, → *L. communis* (d'Orbigny, 1826) var. *gracillima* Cushman, 1936.

*Lepidocyclina gigas* Cushman, 1919, var. *flexuosa* Silvestri, 1937 → *L. flexuosa* L. Rutten, 1911.

*Nummulites irregularis* Deshayes, 1838, var. *douvilléi* Flandrin, 1938, → *Nummulites* (*Gümbelia*) *douvilléi* Prever, 1902; → *N. douvilléi* Vredenburg, 1906, and → *N. subirregulariformis* Flandrin, 1938, var. *douvilléi* Flandrin, 1938.

*Operculina alpina* H. Douvillé, 1916, var. *multiseptata* Silvestri, 1937, → *O. bartschi* Cushman, 1921, var. *multiseptata* Yabe and Hanzawa, 1930.

An example of secondary homonyms may be drawn from the fusulinid Foraminifera. Dunbar and Skinner (1937, p. 711) allocate *Fusulinella meeki* var. *robusta* Dunbar and Condra, 1928, to the genus *Fusulina* Fischer, 1829. The name-combination thus became, through this reallocation, *Fusulina meeki* var. *robusta* (Dunbar and Condra) Dunbar and Skinner. In 1864, however, Meek had named a species *Fusulina robusta*. The reallocation thus created a homonym, even though Meek's species had since been transferred to another genus, *Pseudoschwagerina* Dunbar and Skinner, 1936.

Another case of secondary homonyms is the following: Krotow described in 1898 a form as *Schwagerina fusiformis*. Schellwien, in 1909, published a different form under the name *Fusulina vulgaris* Schellwien, var. *fusiformis*. Finally, in 1934, Chen erected another form, different from either of the above-mentioned ones, as *Pseudofusulina tschernyschewi* (Schellwien) var. *fusiformis*. Dunbar and Skinner (1937, p. 705, 706) referred Krotow's species to the genus *Pseudoschwagerina*, while the two varieties of Schellwien and Chen were allocated to the genus *Schwagerina*. The result of this reallocation is that both are now without a valid name because they became secondary homonyms of *Schwagerina fusiformis* Krotow, 1898, irrespective of the fact that this latter form is now placed into the genus *Pseudoschwagerina*. These homonyms should have been straightened out by the systematists who made the change of generic names on biological grounds.

A third example is presented by *Marginulina texana* Cushman, 1937. This species name was antedated by two days by *Marginulina texana* Garrett and Ellis, 1937. Cushman, in 1938, changed the name of his species to *Marginulina texasensis*. This becomes now a secondary homonym of *Marginulina fragaria* (Gümbel, 1868) var. *texasensis* (Cushman and Applin, 1926), originally named under the generic term *Cristellaria*.

The writer is of the opinion that secondary homonyms among varieties should be treated nomenclaturally like species. The Commission on Zoological Nomenclature might, however, decide that the following is a better solution of the problem:

Although a primary homonym has no nomenclatural validity, a secondary homonym may be retained upon removal to a genus and species in which homonymy does not occur, provided that a substitute name has not been proposed before removal of the secondary homonym from that genus and species in which homonymy occurred. If a secondary homonym is renamed before removal to a genus and species in which homonymy does not occur it can not be retained, but must be replaced by the next valid name.

#### CONCLUSION

The rapid increase in the names applied to the Foraminifera and more intense study of their morphology, classification, and distribution, have caused many problems of classification and nomenclature. Some of these problems have been introduced by students who are unfamiliar with earlier contributions; others are brought about by systematists who revise classifications. Some confusion might be avoided if the International Commission on Zoological Nomenclature would render needed opinions. Stable nomenclature might also be furthered if modern workers would strictly adhere to the Rules. If specialists would carefully consider the problems summarized in this paper and could reach an agreement on course of action, they might avoid the creation of homonyms or they would grant permission to other specialists to rebaptize their illegitimate nomenclatural twins in order to "unscramble many scrambled nomenclatural eggs."

Finally, the principal objective of nomenclature, proper naming so that names will be meaningful and useful, is not lost sight of in the course of focusing attention upon certain nomenclatorial problems. Stable names should be applied to organisms so that the same name-combination will refer to the same assemblage of individual organisms.

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## Nomina Bradyana Mutata

Hans E. Thalmann

In order to complete the list of change of names, or new names, in H. B. Brady's well-known atlas of the Foraminifera of the "Challenger" Expedition (London, 1884), already enumerated in three former papers (Thalmann, 1932, 1933, and 1937), the following record includes such names which have been proposed since 1937, together with previously omitted *nomina mutata* by various authors. They are as follows:

Brady's plate	Brady's figure(s)	<i>nomen mutatum</i>
1	12	<i>Nubecularia lucifuga</i> Defrance, 1925, var. <i>lapidea</i> Wiesner, 1923.
7	5, 6	<i>Pseudomassilina macilenta</i> (Brady, 1884).
8	12	<i>Præmassilina arenaria</i> (Brady, 1884).
14	9	<i>Cyclorbiculina compressa</i> (d'Orbigny, 1839).
23	9, 10	<i>Hyperammina laevigata</i> J. Wright, 1891.
32	13-18	<i>Liebusella soldanii</i> (Jones and Parker, 1860).
35	18, 19	<i>Tholosina vesicularis</i> (Brady, 1884) var. <i>erecta</i> Heron-Allen and Earland, 1929.
36	1-3	<i>Placopsilina bradyi</i> Cushman and McCulloch, 1939.
42	23	<i>Gaudryina</i> ( <i>Siphogaudryina</i> ) <i>rugulosa</i> Cushman, 1932.
42	24	<i>Textularia indenta</i> Galloway and Heminway, 1941.
42	25-29	<i>Gaudryina</i> ( <i>Siphogaudryina</i> ) <i>siphonifera</i> (Brady, 1881).
43	15-19	<i>Textularia orbica</i> Lalicker and McCulloch, 1940.
44	5	<i>Dorothia pseudoturris</i> (Cushman, 1922).
46	1-4	<i>Karrerella bradyi</i> (Cushman, 1911).
46	5, 6	<i>Karrerella chilostoma</i> (Reuss, 1852).
46	12	<i>Karrerella pseudofiliformis</i> (Cushman, 1911). [This same figure was also chosen by Cushman as the type species for <i>Dorothia exilis</i> Cushman, 1936. Since Brady's figure was indicated to represent the type species of <i>Gaudryina pseudofiliformis</i> Cushman, 1911, (which is a new name for <i>G. filiformis</i> Brady, 1884 (non Berthelin, 1880)), it can not be applied to <i>Dorothia exilis</i> Cushman, 1936. The latter name, therefore, becomes a <i>nomen deletum</i> .]
46	17-19	<i>Karrerella</i> ( <i>Karrerulina</i> ) <i>apicularis</i> (Cushman, 1911). Subgenotype of <i>Karrerulina</i> Finlay, 1940.
47	8-12	<i>Eggerella propinqua</i> (Brady, 1884).
47	13, 14	<i>Eggerella affixa</i> (Cushman, 1911).
47	15-17	<i>Eggerella scabra</i> (Williamson, 1858).
47	21-24	<i>Frankeina variabilis</i> (Brady, 1884), according to Finlay, 1939. Franke, 1928, proposed <i>Ammobaculites</i> , and Bartenstein and Brand, 1937, <i>Triplasia</i> for Brady's figures.
48	3, 4, 7, 8, 13	<i>Schenckella communis</i> (d'Orbigny, 1826).
48	19-21	<i>Pseudoclavulina humilis</i> (Brady, 1884).
48	32-38	<i>Liebusella bradyi</i> (Cushman, 1911).
49	10, 11	<i>Clavulinoides indiscretus</i> (Brady, 1881).

- 49 12 *Angulogerina* ? (an *Triplasia* ?) *lepidia* (Brady, 1881).
- 50 1-4 *Bulimina* PARKERAE Thalmann nom. nov. According to Cushman and Parker, 1940, (Contr. Cushman Lab. Foram. Research, vol. 16, p. 14), this species, *Bulimina elegans* Brady, 1884, (non d'Orbigny, 1826), is a synonym of *Bulimina baccata* Fornasini, 1901. As Fornasini's name, however, is already pre-occupied by Yokoyama, 1890, for a "Cretaceous" [in reality is Miocene, according to H. G. Schenck (1936, p. 87)], the new name *B. parkerae* is herewith proposed for Brady's figures.
- 50 18 *Robertina subteres* (Brady, 1884).
- 52 20, 21 *Bolivina spathulata* (Williamson, 1858).
- 52 22 *Loxostomum porrectum* (Brady, 1881).
- 52 23-25 *Bolivina subspinescens* Cushman, 1922.
- 52 26-28 *Loxostomum limbatum* (Brady, 1881).
- 53 1 *Bolivina bradyi* Asano, 1938.
- 53 19-21 *Loxostomum harrarianum* (Brady, 1881).
- 53 22, 23 *Loxostomum amygdalaeforme* (Brady, 1881).
- 59 6 *Lagena crebra* Matthes, 1939.
- 61 28-31 *Glandulonodosaria radícula* (Linné, 1767).
- 62 3 *Ellipsonodosaria rotunda* (d'Orbigny, 1846).
- 62 19-20 *Nodosaria inornata* (d'Orbigny, 1846) var. *bradyensis* Dervieux, 1893.
- 64 1-5 *Pseudoglandulina comatula* (Cushman, 1923).
- 65 16 *Lingulonodosaria bradyi* Silvestri, 1902.
- 66 20 *Nodosariopsis bradyi* Silvestri, 1902.
- 75 18-20 *Rectobolivina bifrons* (Brady, 1881).
- 91 1 *Epistomaria polystomelloides* (Parker and Jones, 1865).
- 91 4 *Discorbis rugosa* (d'Orbigny, 1839) var. *minuta* Schubert, 1904.
- 95 5 *Cibicides bradyi* (Trauth, 1918).
- 104 4, 5 *Laticarinina halophora* (Stache, 1864).
- 106 7 *Canceris philippinensis* (Cushman, 1921).
- 107 8, 9 *Notorotalia clathrata* (Brady, 1876).
- 108 8, 9 *Tinoporus hispidus* (Brady, 1876).
- 109 22 *Elphidium subgranulosum* Asano, 1938.
- 113 6 *Pseudobulimina convoluta* (Williamson, 1858).
- 113 7 *Loxostomum strigosum* (Brady, 1884).
- 113 14 *Schubertia limbata* (Brady, 1884).

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## A Key to the Genera of the Anacardiaceae

Fred A. Barkley

Since the publication of the key to the genera of the Anacardiaceae by Engler in Engler & Prantl's *Die natürlichen Pflanzenfamilien* 3(5):138-178 in 1892 there seems to have been no publication of such a key. Although the writer is in the early stages of a study of the family, so that such a key of necessity must be prepared from literature, it appears that the publication of a tentative key to the genera of the family would be of value.

Fossil species have been published which would be assigned to the genera *Rhus*, *Schmaltzia*, *Toxicodendron*, *Searsia*, *Pistacia*, *Metopium* and *Schinus*. The following genera of fossils have been assigned to the family: *Spondiocrarpum* Warburg 1897, *Anacardiophyllum* Ettingshausen 1869 (*Anacardites* Saporta in Heer 1861), *Daphnophyllum* Heer 1874, *Trilobium* Saporta in Heer 1861 (*Heterocalyx* Saporta 1873, *Getonia* Unger 1847), *Folliculites* Zenker 1833, *Rhoipites* Wodehouse 1933, *Anacardioxylon* Felix 1882, *Semecarpites* Fritel 1912, *Teschia* Reid & Reid 1915, *Protamyris* Unger ex Schimper 1850, *Sumatroxylon* Berger 1923. Since in several cases their relationship to this family is problematical and in most cases the fossils are sufficiently incomplete so that their position in the family is obscure, they have been omitted from the following key.

References to the literature have been omitted since reference to de Dalla Torre & Harm's *Genera Siphonogamarum*, Hooker & Jackson's *Index Kewensis*, the *Gray Card Catalogue*, and the *Compendium of Fossil Botany* in the United States Geological Survey will give the complete references. The author is grateful to the Penrose Fund of the American Philosophical Society for grants-in-aid which have allowed for the assembling of literature for monographic studies in the Anacardiaceae which have made this key possible.

Several genera variously listed as being Anacardiaceous (*Rumphia* Linnaeus 1753, (*Tsiemtani* Adans. 1763), *Triceros* Lour. 1790, *Huertea* Ruiz & Pavon 1794 (*Huertia* G. Don 1832), *Juliania* Schlecht. 1843 (*Hypopterygium* Schlecht. 1843), *Blepharocarya* F. Muell. 1878, *Garugandra* Griseb. 1879, and *Rhodosphaera* Engl. 1881) have been omitted since they appear to belong to other families.

The author proposes that *BUCHANANIA* Spreng., *Schrad. Journ.* 2:234. 1800, be conserved over *Launzan* Buch.-Ham., *Asiat. Research* 5:123. 1799, since *Buchanania* has been the name used almost universally in monographic studies, floras and botanical indices for the genus concerned during the past century. In the three following cases disregard of the Adanson names would eliminate much confusion: *ANACARDIUM* [Linnaeus] Rottböll., *Act. Hafn.* 2:252. 1775 (*Acajou* [Tournefort] Adans., *Fam.* 2:344. 1763); *HOLIGARNA*

Buch.-Ham. ex Roxb., *Hort. Bengal.* 22: 1814 (*Katoutsjeroe* Adans., *Fam.* 2:534. 1763); ODINA Roxb., *Hort. Bengal.* 29. 1814 (*Calesiam* Adans., *Fam.* 2:446. 1763).

1. Only one carpel, the female flower completely naked, leaves opposite, simple, serrate. Himalayan region. .... DOBINEAE, *Dobinia* 1
1. Carpels free or united, or if only one, then leaves simple, entire.
  2. Five free carpels, or only one carpel. .... MANGIFEREAE
  3. Carpels usually five, usually only one fertile; drupe more or less lenticular.
    4. Anthers not inflexed, stigma not sessile. Malayan region. .... *Buchanania* 2
    4. Anthers inflexed, stigma sessile. Borneo. .... *Androtium* 3
  3. Carpel one.
    4. Leaves opposite; stamens the same number as petals; drupe ovoid. Malayan region. .... *Bouea* 4
    4. Leaves alternate.
      5. Stamens in one to four cycles; drupe small, globose, on a gynophore; petals enlarged in fruit. Malayan region. .... *Melanorrhoea* 5
      5. Not as above.
        6. Stamens five, fertile; drupe globose or ovoid.
          7. Petals deciduous, not enlarging. Malayan region. .... *Gluta* 6
          7. Petals in fruit enlarged. Malayan region. .... *Swintonia* 7
        6. Stamens ten or five, only four to one fertile, the rest more or less abortive (seldom five fertile in *Mangifera*).
          7. Drupe reniform or ovoid, with soft mesocarp, a hard fibrous endocarp and only a little thickened gynophore.
            8. Sepals in one whorl. East Indian and Malayan regions. .... *Mangifera* 8
            8. Sepals in two whorls. West Africa. .... *Fegimanra* 9
          7. Drupe reniform, compressed, with a hardened fruit wall and much thickened and enlarged gynophore. Tropical America. .... *Anacardium* 10
  2. Carpels united into a compound pistil; leaves seldom simple.
    3. Carpels usually five or four, seldom more or only three; each carpel developing a cavity in fruit, which bears a single seed from its upper end. .... SPONDIEAE

1 *Dobinea* Buch.-Ham. ex D. Don 1825 (*Dobinea* Spreng. 1826).

2 *Buchanania* Spreng. 1800 (*Launzan* Buch.-Ham. 1799, *Lanzana* Stokes 1812, *Cambessedea* Kunth 1824, *Lundia* Puer. ex de Candolle 1825, *Coniogeton* Blume 1826, *Hypericinea* Wall. 1831, *Larmzon* Roxb. 1832, *Launzea* Endl. 1841, *Buchaniana* Pierre 1898).

3 *Androtium* Hooker 1905.

4 *Bouea* Meissn. 1837 (*Manga* Noronha 1790 non *Mangas* Adans 1763, *Canbesedea* Wight et Arn. 1834).

5 *Melanorrhoea* Wall. 1829.

6 *Gluta* Linnaeus 1771 (*Stagmaria* Jack 1823, *Syndesmis* Wall., in Roxburgh 1824).

7 *Swintonia* Griff. 1846 (*Astropetalum* Griff. 1854, *Anauxanopetalum* Teijsm. et Binn. 1861).

8 *Mangifera* Linnaeus 1753 (*Mangas* Adans. 1763, *Marchandora* Pierre 1897).

9 *Fegimanra* Pierre 1892.

10 *Anacardium* [Linnaeus] Rottböll 1775 (*Acajou* [Tourn.] Adans. 1763, *Cassuvium* Lam. 1783, *Acajuba* Gaertn. 1788, *Fabrenia* Noronha 1790, *Trima* Noronha 1790, *Rhinocarpus* Bert. et Balb. ex Humboldt, Bonpland et Kunth 1825, *Monodynamus* Pohl 1831, *Anacardia* St.-Lag. 1880).

4. Embryo curved, with cotyledons against the radical; style absent, stigmas sessile, subapical on each carpel. Tropical America. .... *Tapirira* 11
4. Embryo straight, with short straight radical.
  5. Petals valvate; leaflets with a nerve around the outer edge.
    6. Pistil formed from five carpels.
      7. Leaves compound.
        8. Radical horizontal; style short. Western Africa. .... *Antrocaryon* 12
        8. Radical not horizontal. Tropical regions. .... *Spondias* 13
      7. Leaves simple. Africa. .... *Spondianthus* 14
    6. Pistil not formed from five carpels.
      7. Carpels four. Africa. .... *Nothospondias* 15
      7. Carpel one. East Indies. .... *Solenocarpus* 16
  5. Petals imbricate.
    6. Petals valvate below, with the apex imbricate and thickened. India and the Malayan region. .... *Dracontomelum* 17
    6. Petals completely imbricate in the bud.
      7. Flower three-parted. West Africa. .... *Haematostaphis* 18
      7. Flower four to five parted.
        8. Style terminal, four or five parted at the apex.
          9. Sepals and petals five. Mexico. .... *Cyrtocarpa* 19
          9. Sepals and petals four. Africa. .... *Spondiopsis* 20
        8. Style in the perfect flowers usually at the side of the ovary.
          9. Hilum spatula shaped. Australia. .... *Pleiogynium* 21
          9. Hilum shield shaped.
            10. Sepals free.
              11. Anthers long, basifixed. Tropical Africa. .... *Sclerocarya* 22
              11. Anthers round, versitile. Tropical Africa. .... *Pseudospondias* 23
            10. Sepals more or less united at the base.
              11. Corolla four parted; fruit four, or through abortion one to three celled, one seeded; shrubs and trees. Tropical Africa and the East Indies. .... *Odina* 24

11 *Tapirira* Aubl. 1775 (*Jonquetia* Schreb. 1789, *Jonquetia* Schreb. 1789, *Tapirira* Juss. 1789, *Salabertia* Neck. 1790, *Tapinia* Steud. 1841).

12 *Antrocaryon* Pierre 1898.

13 *Spondias* Linnaeus 1753 (*Monbin* [Plum.] Adans. 1763, *Evia* Comm. ex Jussieu 1789, *Cytheraea Chrysomelon* Forst. ex A. Gray 1854, *Warmingia* Engl. 1874).

14 *Spondianthus* Engler 1905.

15 *Nothospondias* Engler 1905.

16 *Solenocarpus* Wight. et Arn. 1834.

17 *Dracontomelum* Blume 1850 (*Comeurya* Baill. 1872).

18 *Haematostaphis* Hook. f. 1860.

19 *Cyrtocarpa* Humbolt, Bonpland, et Kunth 1825 (*Dasycarya* Liebm. 1853).

20 *Spondiopsis* Engler 1905.

21 *Pleiogynium* Engler 1883 (*Pliogynopsis* Kuntze 1903).

22 *Sclerocarya* Hochst. 1844 (*Sclerocarpa* Sonder 1850).

23 *Pseudospondias* Engler 1883.

24 *Odina* Roxb. 1814 (*Calesiam* Adans. 1763, *Calesia* Rafinesque 1814, *Haberlia* Dennst. 1818, *Calesiama* Rafinesque 1838, *Lannea* A. Rich. in Guillemin et Perrotet 1832, *Wirtgenia* Jungh. ex Hasskarl. 1844, *Kokkia* Zipp. ex Blume 1850, *Calesium* Kuntze 1891).

11. Corolla five parted.
12. Stone fruit five, or through abortion three celled; five to three seeded; sepals five parted. Maritius.  
..... *Poupartia*<sup>25</sup>
12. Fruit not five or three celled at maturity.
13. Fruit two celled at maturity; tree. South Africa.  
..... *Harpephyllum*<sup>26</sup>
13. Fruit usually a one celled drupe.
14. Climbing shrub. Himalayan region..... *Pegia*<sup>27</sup>
14. Tree. Malayan region. .... *Koordersiodendron*<sup>28</sup>
3. Carpels three (possibly only one in *Pentaspadon*); ovary with only one seed bearing locule, the two other small or absent.
4. Ovary seldom free (*Glycycarpus*), sunken in a cup shaped or tubular hollowed receptacle. .... *SEMECARPEAE*
5. Styles three, apical.
6. Stigmas globular.
7. Ovary in the pistillate flowers superior or half-inferior; petiole without side splitting. India to Australia. .... *Semecarpus*<sup>29</sup>
7. Ovary in the pistillate flowers inferior; petiole with one to two lateral splits at the base. East Indies. .... *Holigarna*<sup>30</sup>
6. Stigmas bilobed. Borneo. .... *Melancommia*<sup>31</sup>
5. Style short, apical with three parted stigma.
6. Receptacle not enlarged in the mature fruit; corolla four-parted. East Indies. .... *Glycycarpus*<sup>32</sup>
6. Receptacle not enlarged in the mature fruit; corolla five parted.
7. Receptacle shortly cup shaped, the lower part of the corolla hardly included; calyx very thickly hairy, valvate. Malacca..... *Melanochyla*<sup>33</sup>
7. Receptacle cup shaped; the fruit mostly enclosed; calyx wide, ovoid, imbricate. Himalayan region. .... *Drimycarpus*<sup>34</sup>
4. Ovary and fruit free; leaves various. .... *RHOIDEAE*
5. Flowers with simple, homeochlamydic perianth or naked.
6. Ovary compressed; three small stigmas on the side of the upper end; leaves simple. Peru. .... *Haplorhus*<sup>35</sup>

25 *Poupartia* Comm. ex Jussieu 1789 (*Shaku* Boj. 1837).

26 *Harpephyllum* Bernh. ex Krauss 1844.

27 *Pegia* Colebr. 1827 (*Robergia* Roxb. 1832, *Phlebochiton* Wall. 1835).

28 *Koordersiodendron* Engler in Koorders 1898.

29 *Semecarpus* Linnaeus f. 1781 (*Oncocarpus* A. Gray 1854, *Semecarpus* St.-Lag. 1880).

30 *Holigarna* Buch.-Ham. ex Roxburgh 1814 (*Katoutsjeroc* Adans. 1763, *Hades-taphylum* Dennst. 1818, *Catutsjeron* Kuntze 1891).

31 *Melancommia* Ridley 1933.

32 *Glycycarpus* Dalz. 1849 (*Nothopegia* Blume 1850, *Glycycarpus* Benth. et Hook. f. 1862).

33 *Melanochyla* Hook. f. 1876.

34 *Drimycarpus* Hook. f. 1862.

35 *Haplorhus* Engl. 1881.



6. Ovary almost globose or shortly ovoid; style shortly three divided, three large long inverted egg-shaped stigmas. Mediterranean region, East Indies, and Mexico. .... *Pistacia*<sup>36</sup>
5. Flowers with double or heteroecious perianth.
  6. With two cycles of stamens, one fertile and one sterile; leaves imparipinnate.
    7. Seed upright; stigma one, bending to one side. Sumatra... *Pentaspadon*<sup>37</sup>
    7. Seed suspended; stigmas globose, three parted. Malacca... *Microstemon*<sup>38</sup>
  6. With as many, or twice as many (seldom more) stamens as petals.
    7. Receptacle deeply cup shaped; petals scarcely longer and broader than the sepals; ovary two to three celled; leaves imparipinnate. Amazonian region. .... *Thyrsoedium*<sup>39</sup>
    7. Receptacle flat or developed into a disk between the ovary and stamens; seldom hollow and rarely a gynophore present.
      8. Embryo straight, with very short radical; stamens as many or twice as many as the petals; seed suspended; leaves pinnate.
        9. Fruit held up by a long compressed gynophore; stamens as many as the petals. Madagascar. .... *Faguetia*<sup>40</sup>
        9. Fruit a sessile drupe.
          10. Calyx in fruit greatly enlarged, winged; stamens as many as the petals. Malayan region. .... *Parishia*<sup>41</sup>
          10. Calyx in fruit not enlarged.
            11. Stamens hypogynous, as many to more than twice as many as the petals. Africa and South America. .... *Sorindeia*<sup>42</sup>
            11. Stamens epipetalous, as many as the petals. Tropical Africa. .... *Trichoscypha*<sup>43</sup>
      8. Embryo more or less bent, with the cotyledons free or laying against the radical.
        9. Ovary two to three celled.
          10. Two to three cells of the ovary with only one seed hanging from the middle of the wall; fruit one seeded; embryo with a short slightly bent radical; stamens five.
            11. Leaves opposite or subopposite; calyx five parted. Madagascar and Africa. .... *Protorhus*<sup>44</sup>
            11. Leaves alternate; calyx three parted. North Africa. .... *Scassellatia*<sup>45</sup>

36 *Pistacia* Linnaeus 1753 (*Lentiscus* [Tourn.] Mill. 1754, *Terebinthus* Mill. 1754, *Euvardia* Adans. 1763, *Pistachia* Salisb. 1796, *Terminthos* St.-Lag. 1881, *Therminthos* St.-Lag. 1881).

37 *Pentaspadon* Hook. f. 1860 (*Nothoprotium* Miq. 1860).

38 *Microstemon* Engler 1881.

39 *Thyrsoedium* Salzm. ex Benth. 1852.

40 *Faguetia* Marchand 1869.

41 *Parishia* Hook. f. 1860.

42 *Sorindeia* P. Thou. 1806 (*Dupuisia* A. Rich. in Guillemin et Perrottet 1832.

*Sorindeiopsis* Engl. 1905).

43 *Trichoscypha* Hook. f. 1862 (*Tricoscypha* Engl. in D. C. 1883, *Emiliomarcelia*

Th. et A. Dur. ex Chevalier 1912).

44 *Protorhus* Engler 1881.

45 *Scassellatia* Chiovenda 1932.

10. Ovary imperfectly two celled, with one fertile cell; seed hanging from the apex; embryo very curved with a long radical and the cotyledons wound about the sterile cell. East Indies, Tropical Africa and Brazil. *Camptosperma* 45a
9. Ovary one celled.
  10. Embryo with free, short or long radical; stamens twice as many as the petals; seed suspended.
    11. Petals valvate, sepals truncate. New Caledonia. .... *Montagueia* 46
    11. Petals imbricate, sepals not truncate. New Caledonia and Australia. .... *Euroschinus* 47
  10. The radical of the embryo laying against the cotyledons.
    11. Flowers with twice as many stamens as petals.
      12. Seed suspended.
        13. Endocarp of the drupe thin, parchment like. Andes of South America. .... *Mauria* 48
        13. Endocarp of the drupe bony.
          14. Fruit globose. South America. .... *Schinus* 49
          14. Fruit compressed. Lower California. .... *Pachycormus* 50
      12. Seed basal. South America. .... *Lithraea* 51
    11. Flowers with as many stamens as petals.
      12. Drupe compressed upwards into a wing; style lateral on the fruit.
        13. The entire fruit wall thin, perianth five parted. South America. .... *Loxopterygium* 52
        13. The epicarp thin, endocarp thick and bony. South America. .... *Schinopsis* 53
      12. Drupe not winged or with a wing all around.
        13. Style or stigma lateral on the fruit.
          14. Seed basal in the ovary.
            15. Petals obtuse; perianth in fruit not enlarged; leaves simple; (pedicels of the sterile flowers at length becoming plumose). Asia, Europe and North America. .... *Cotinus* 54

45a *Camptosperma* Thwait 1854 (*Cyrtospermum* Benth. 1852 non *Cyrtosperma* Griff. 1851, *Drepanospermum* Benth. et Hook. f. 1862).

46 *Montagueia* Baker f. 1921.

47 *Euroschinus* Hook. f. 1862.

48 *Mauria* Kunth 1824.

49 *Schinus* Linnaeus 1753 (*Molle* [Tourn.] Adans. 1763, *Duvaia* Kunth 1824, *Duaiva* Tenore 1845, *Sarcotheca* Turcz. 1858, *Schinos* St.-Lag. 1880).

50 *Pachycormus* Coville 1911 (*Veatchia* A. Gray 1885 non Kellogg 1863).

51 *Lithraea* Miers 1826 (*Litria* G. Don 1833, *Lithrea* Hook. 1833, *Litrea* Phil. 1864).

52 *Loxopterygium* Hook. f. 1862.

53 *Schinopsis* Engl. in Mart. et Eichl. 1876 (*Quebrachia* Griseb. 1879).

54 *Cotinus* [Tourn.] Mill. 1754.

- 15. Petals acute; perianth enlarged and enclosing the fruit; leaves imparipinnate.  
South Africa. .... *Loxostylis* 55
- 14. Seed suspended from the top of the ovary.
  - 15. Pedicels of the pistillate flowers finally spreading; style one; leaf simple.  
South Africa. .... *Laurophyllus* 56
  - 15. Pedicels always thin.
    - 16. Stigmas three, styles three; fruit with a broadly winged band. Africa. ....  
..... *Smodingium* 57
    - 16. Style one; fruit without broadly winged band. Madagascar. ....  
..... *Micronychia* 58
- 13. Stigma or style more or less at the apex of the ovary.
  - 14. Calyx in fruit enlarging; layers of the fruit wall not finally separating. South America. .... *Astronium* 59
  - 14. Calyx in fruit not enlarging.
    - 15. Layers of the fruit-wall not finally separating.
      - 16. Endocarp thin.
        - 17. Leaves simple. Madagascar. .... *Baronia* 60
        - 17. Leaves pinnate.
          - 18. Leaves sinuate spinose. Tropical America.  
..... *Comocladia* 61
          - 18. Leaves entire. West Indies. .... *Metopium* 62
      - 16. Endocarp thick, bony; mesocarp fleshy.
        - 17. Leaves simple. Africa. .... *Heeria* 63
        - 17. Leaves compound. West Indies and Central America. .... *Mosquitoxylum* 64
    - 15. Layers of the fruit wall finally separating in various ways; seed basal.
      - 16. Drupe strongly compressed; leaves imparipinnate.
        - 17. Drupe reniform, margin not pilose. Mexico.  
..... *Pseudosmodingium* 65
        - 17. Drupe cordate, margin long pilose. Colombia.  
..... *Ochoterenaca* 66

- 
- 55 *Loxostylis* Spreng. ex Reichenbach 1827 (*Anasyllis* E. Mey. in Drège 1843).
  - 56 *Laurophyllus* Thunb. 1792 (*Botryceras* Willd. 1811, *Laurophyllus* Roem. et Schult. 1818, *Daphnites* Spreng. 1825, *Laurophyllum* Göppert 1853).
  - 57 *Smodingium* E. Mey. 1843.
  - 58 *Micronychia* Oliver 1881.
  - 59 *Astronium* Jacq. 1760 (*Myracrodruon* Freire Allemão ex Engl. 1881).
  - 60 *Baronia* Baker 1882.
  - 61 *Comocladia* Linnaeus 1756 (*Comocladia* Linnaeus 1762, *Dodonaea* [Plum.] Adans. 1763, *Brasilistrum* Lam. 1783, *Brasilium* J. F. Gmel. 1791).
  - 62 *Metopium* P. Br. 1756.
  - 63 *Heeria* Meissn. 1837 (*Roemaria* Thunb. 1798 non Moench. 1794, *Anafrenium* Arn. in Hooker 1841, *Anaphrenium* E. Mey. ex Endlicher 1841).
  - 64 *Mosquitoxylum* Krug et Urban 1895.
  - 65 *Pseudosmodingium* Engler 1881.
  - 66 *Ochoterenaca* Barkley 1942.

16. Drupe never so compressed as to appear winged; leaves simple, ternate or imparipinnate.
17. Ovary upon a gynophore formed by the disk; epicarp clothed with filiform silky hairs over three mm. long. Mexico. .... *Actinocheita*<sup>67</sup>
17. Ovary not upon a column; epicarp when clothed with hairs, with hairs less than one and a half mm. long.
18. Drupes red, noticeably pubescent with red glandular hairs.
19. Flowers in dense terminal thyrsi, appearing after the leaves; bracts linear lanceolate, deciduous, one subtending each flower; bracteoles absent; branches thick. Asia, Europe and North America. .... *Rhus*<sup>68</sup>
19. Flowers in terminal and lateral compound spikes, appearing with or before the leaves; bracts deltoid or ovate, persistent, one bract and two bracteoles subtending each flower. North America. .... *Schmaltzia*<sup>69</sup>
18. Drupes white, black, or dun-colored; glabrous or sparingly pubescent, pubescence on fruit never glandular.
19. Drupes black, glabrous; exocarp and mesocarp adhering. East Indies. .... *Duckera*<sup>70</sup>
19. Drupes white or dun-colored, glabrous or sparingly pubescent; mesocarp and endocarp adhering.
20. Mesocarp not waxy, but resinous; leaves usually ternate. South Africa. .... *Searsia*<sup>71</sup>
20. Mesocarp waxy; leaves usually simple or pinnately compound.
21. Sterile carpels forming a line down the side of the fruit; drupe very small; mesocarp without fibers; leaves coriaceous, simple; inflorescence a

<sup>67</sup> *Actinocheita* Barkley 1937.

<sup>68</sup> *Rhus* Linnaeus 1753.

<sup>69</sup> *Schmaltzia* Desv. 1813 (*Turpinia* Raf. 1808 non Vent. 1803, *Lobadium* Rafinesque 1819, *Styphonia* Nuttall 1838, *Schmalzia* Desv. 1841, *Stiphonia* Hemsl. 1880, *Rhocidium* Greene 1905, *Neostyphonia* Shafar in Britton 1908).

<sup>70</sup> *Duckera* Barkley 1942 (*Duckera* n. gen. = (*Rhus*) Section MELANOCARPAE Engl., *Bot. Jahrb.* 1:380. 1881. Named after Elizabeth Ducker Barkley).

<sup>71</sup> *Searsia* Barkley 1942 (*Searsia* n. gen. = (*Rhus*) Section GERONTOGEAE Engl., *Bot. Jahrb.* 1:379. 1881. Named after Paul B. Sears).

terminal thyrsus; innocuous  
evergreen shrub. California.

.....*Malosma* 72

21. Sterile carpels not detectable at maturity; drupes over 2.2 mm. in diameter; mesocarp with "fibers"; leaves thin, ternate or imparipinnate; inflorescence a lateral panicle; poisonous, deciduous small trees, shrubs or vines. Asia and North America. ....  
.....*Toxicodendron* 73

72 *Malosma* Engler in D.C. 1883.

73 *Toxicodendron* [Tourn.] Mill. 1754 (*Vernix* Adans. 1763, *Rhus-Toxicodendron* Marsh 1785, *Pocophorum* Neck. 1790, *Philostemon* Rafinesque 1817, *Philostemum* Steud. 1841).

Table of Synonymy and Index of Accepted Genera (Numbers in Italics refer to footnotes).

<i>Acajou</i> = <i>Anacardium</i>	<i>Chrysomelon</i> = <i>Spondias</i>	<i>Glycicarpus</i> = <i>Glycycarpus</i>
<i>Acajuba</i> = <i>Anacardium</i>	<i>Comacladia</i> = <i>Comocladia</i>	<i>Glycycarpus</i> 5, 32
<i>Actinocheita</i> 67	<i>Comocladia</i> 61	<i>Haberlia</i> = <i>Odina</i>
<i>Anacardia</i> = <i>Anacardium</i>	<i>Coniogeton</i> = <i>Buchanania</i>	<i>Hadestaphylum</i> = <i>Holigarna</i>
<i>Anacardiophyllum</i> 1	<i>Cotinus</i> 54	<i>Haematostaphis</i> 18
<i>Anacardioxylon</i> 1	<i>Cytheraea</i> = <i>Spondias</i>	<i>Haplorhus</i> 35
<i>Anacardites</i> = <i>Anacardio-</i>	<i>Cyrtocarpa</i> 19	<i>Harpephyllum</i> 26
<i>phyllum</i>	<i>Cyrtospermum</i> = <i>Campos-</i>	<i>Heeria</i> 63
<i>Anacardium</i> 1, 10	<i>permum</i>	<i>Heterocalyx</i> = <i>Trilobium</i>
<i>Anafrenium</i> = <i>Heeria</i>	<i>Daphintes</i> = <i>Laurophyllum</i>	<i>Holigarna</i> 1, 30
<i>Anaphrenium</i> = <i>Heeria</i>	<i>Daphnophyllum</i> 1	<i>Huertea</i> 1
<i>Anasyllis</i> = <i>Loxostylis</i>	<i>Dasycarya</i> = <i>Cyrtocarpa</i>	<i>Huertia</i> = <i>Huertea</i>
<i>Anauxanopetalum</i> = <i>Swin-</i>	<i>Dobinaca</i> = <i>Dobinia</i>	<i>Hypericinea</i> = <i>Buchanania</i>
<i>tonia</i>	<i>Dobinia</i> 1	<i>Hypopterygium</i> = <i>Juliania</i>
<i>Androtium</i> 3	<i>Dodonaea</i> = <i>Comocladia</i>	<i>Jonquetia</i> = <i>Tapirira</i>
<i>Antrocaryon</i> 12	<i>Dracontomelum</i> 17	<i>Juliania</i> 1
<i>Astronium</i> 59	<i>Drepanospermum</i> = <i>Camp-</i>	<i>Katoutsjeron</i> = <i>Holigarna</i>
<i>Astropetalum</i> = <i>Swintonia</i>	<i>nosperma</i>	<i>Kokkia</i> = <i>Odina</i>
<i>Baronia</i> 60	<i>Drimycarpus</i> 34	<i>Koordersiodendron</i> 28
<i>Blepharocarya</i> 1	<i>Duauva</i> = <i>Duvaua</i>	<i>Lannea</i> = <i>Odina</i>
<i>Botryoceras</i> = <i>Laurophyllum</i>	<i>Duckera</i> 70	<i>Lanzana</i> = <i>Buchanania</i>
<i>Bouea</i> 4	<i>Dupuisia</i> = <i>Sorindeia</i>	<i>Larmzon</i> = <i>Buchanania</i>
<i>Brasilistrum</i> = <i>Comocladia</i>	<i>Duvaua</i> = <i>Schinus</i>	<i>Launzan</i> = <i>Buchanania</i>
<i>Brasilium</i> = <i>Comocladia</i>	<i>Emiliomarcelia</i> = <i>Tricho-</i>	<i>Launzea</i> = <i>Buchanania</i>
<i>Buchanania</i> 1, 2	<i>scypha</i>	<i>Laurophyllum</i> = <i>Laurophyllum</i>
<i>Buchaniana</i> = <i>Buchanania</i>	<i>Euroschinus</i> 47	<i>phyllum</i>
<i>Calesia</i> = <i>Odina</i>	<i>Evia</i> = <i>Spondias</i>	<i>Laurophyllum</i> 56
<i>Calesiam</i> = <i>Odina</i>	<i>Evrardia</i> = <i>Pistacia</i>	<i>Lentiscus</i> = <i>Pistacia</i>
<i>Calesiana</i> = <i>Odina</i>	<i>Fabrenia</i> = <i>Anacardium</i>	<i>Lithraea</i> 51
<i>Calesium</i> = <i>Odina</i>	<i>Fagnuetia</i> 40	<i>Lithrea</i> = <i>Lithraea</i>
<i>Camposperma</i> 45a	<i>Fegimandra</i> 9	<i>Litrea</i> = <i>Lithraea</i>
<i>Cambessedea</i> = <i>Buchanania</i>	<i>Folliculites</i> 1	<i>Litria</i> = <i>Lithraea</i>
<i>Cambessedea</i> = <i>Bouea</i>	<i>Garugandra</i> 1	<i>Lobodium</i> = <i>Schmaltzia</i>
<i>Cassivium</i> = <i>Anacardium</i>	<i>Getonia</i> = <i>Trilobium</i>	
<i>Catutsjeron</i> = <i>Holigarna</i>	<i>Gluta</i> 6	

- Loxopterygium* 52  
*Loxostylis* 55  
*Lundia*=*Buchanania*  
*Malosma* 72  
*Manga*=*Bouea*  
*Mangas*=*Mangifera*  
*Mangifera* 2, 8  
*Marchandora*=*Mangifera*  
*Mauria* 48  
*Melancommia* 31  
*Melancohyla* 33  
*Melanorrhoea* 5  
*Metopium* 1, 62  
*Micronychia* 58  
*Microstemon* 38  
*Molle*=*Schinus*  
*Monbin*=*Spondias*  
*Monodynamus*=*Anacardium*  
*Montagueia* 46  
*Mosquitoxylum* 64  
*Myracrodruon*=*Astronium*  
*Neostyphonia*=*Schmaltzia*  
*Nothopegia*=*Glycyecarpus*  
*Nothoprotium*=*Pentaspadon*  
*Nothospondias* 15  
*Ochoterena* 66  
*Odina* 1, 24  
*Oncocarpus*=*Semecarpus*  
*Pachycormus* 50  
*Parishia* 41  
*Pegia* 27  
*Pentaspadon* 5, 37  
*Philostemon*=*Toxicodendron*  
*Philostemon*=*Toxicodendron*  
*Phlebochiton*=*Pegia*  
*Pistachia*=*Pistacia*  
*Pistacia* 1, 36  
*Pleiogynium* 21  
*Pocophorum*=*Toxicodendron*  
*Poupartia* 25  
*Protamyris* 1  
*Protorhus* 44  
*Pseudosmodingium* 65  
*Pseudospondias* 23  
*Quebrachia*=*Schinopsis*  
*Rhinocarpus*=*Anacardium*  
*Rhodospaera* 1  
*Rhoetidum*=*Schmaltzia*  
*Rhoipites* 1  
*Rhus* 1, 68  
*Rhus-Toxicodendron*=*Toxicodendron*  
*Robergia*=*Pegia*  
*Roemeria*=*Heeria*  
*Rumphia* 1  
*Salabertia*=*Tapirira*  
*Sarcotheca*=*Schinus*  
*Scasselatia* 45  
*Schinopsis* 53  
*Schinus*=*Schinus*  
*Schinus* 1, 49  
*Schmaltzia* 1, 69  
*Schmalzia*=*Schmaltzia*  
*Sclerocarpa*=*Sclerocarya*  
*Sclerocarya* 22  
*Searsia* 1, 71  
*Semecarpites* 1  
*Semecarpus*=*Semecarpus*  
*Semecarpus* 29  
*Shakua*=*Poupartia*  
*Smodingium* 57  
*Solenocarpus* 16  
*Sorindeia* 42  
*Sorindeiopsis*=*Sorindeia*  
*Spodias*=*Spondias*  
*Spondianthus* 14  
*Spondias* 13  
*Spondiocarpum* 1  
*Spondiopsis* 20  
*Stagmaria*=*Gluta*  
*Stiphonia*=*Schmaltzia*  
*Styphonia*=*Schmaltzia*  
*Sumatroxylon* 1  
*Swintonia* 7  
*Syndesmis*=*Gluta*  
*Tapinia*=*Tapirira*  
*Tapirira* 11  
*Terebinthus*=*Pistacia*  
*Terminthos*=*Pistacia*  
*Teschia* 1  
*Therminthos*=*Pistacia*  
*Thyrsodium* 39  
*Toxicodendron* 1, 73  
*Triceros* 1  
*Trichoscypha* 43  
*Tricoscypha*=*Trichoscypha*  
*Trilobium* 1  
*Trima*=*Anacardium*  
*Tsiemlani*=*Rumphia*  
*Turpinia*=*Schmaltzia*  
*Veatchia*=*Pachycormus*  
*Vernix*=*Toxicodendron*  
*Warmingia*=*Spondias*  
*Wirtgenia*=*Odina*  
*Wirtgenia*=*Spondias*

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## A Note on Unusual Plants in the Flora of Northwestern Nebraska

W. L. Tolstead

During the past twenty years several unusual, local floras have been described in Canada and the Great Lakes Region (Raup 1941, Fernald 1935). Significant floras remain to be studied in more detail than has been done to this time in regions west of the Mississippi River along broad fronts ahead of the several lobes of glacial deposits and in areas which have escaped glaciation. The flora of the "non-glaciated" region of the Mississippi Valley in southeastern Minnesota and adjacent areas in Iowa and Wisconsin is of special interest, but plants in localities on both the west and east edge of the Des Moines Lobe of late Wisconsin glaciation in northwestern and northeastern Iowa are of equal interest (Cooper 1935, Hayden 1940). The flora of the Black Hills is also important because many eastern and northern plants are here on the western or southern border of their range (McIntosh 1931). The same is true of a large number of rare plants of northern Nebraska, especially in the sand hills, in the Niobrara Valley, and in the canyons of Pine Ridge.

*Dodecatheon amethystinum*, described by Fassett (1931), is an example of a rare plant confined to a limited area. It occurs occasionally on the limestone cliffs of the "non-glaciated" region. Most of the interesting plants, however, are merely outlyers or samples of discontinuous distribution. A study of *Rubus odoratus* and *R. parviflorus* by Fassett (1941) exemplifies this type of distribution. A part of Fassett's study compares outlyers of *Rubus parviflorus* in the Great Lakes Region with specimens from the Rocky Mountains and the Pacific Coast where the greatest development of this species has taken place. A large number of unusual plants of Northern Nebraska is of similar nature. These are mesophytic species, which are now widely separated from their major distribution and occur in a semiarid region because many mesophytic habitats result from the interrelations of local geology, soils, topography, and ground water.

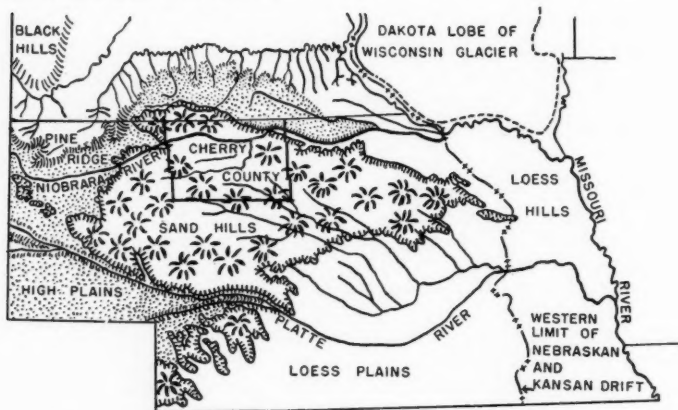
Many of the rare plants were recorded in Nebraska during the years of exploration by Bessey (1898), Rydberg (1895), Bates (1914), and Pool (1913). No full summary, however, has been made of the flora from any special locality, and the nature of the environments which permitted survival of mesophytic plants has not been recorded fully. The history of these unusual communities in light of new information concerning the Pleistocene Geology of Nebraska and adjacent states is reserved as a part of another paper.

### LOCATION AND GENERAL ENVIRONMENT

Cherry County is on the northern boundary of Nebraska, Fig. 1. It is largely sand hills, but the Crookston Table, an area of hardlands, is in its northeastern corner. The deep canyon of the Niobrara drainage is also in the



northern portion of this county. The part of the Niobrara Valley which was studied is east of Valentine, and borders the south edge of the Crookston Table. The sand hills, where special studies were made, are 35 to 50 miles south of the Niobrara River in the vicinity of the Valentine Lakes Refuge. These areas were studied from 1936 to 1938.



Pine Ridge is a topographic region in the northwestern corner of Nebraska, approximately 100 miles south of the Black Hills in South Dakota. It is a zone of rough, stony land and deep canyons between the Dawes Table and the lowlands drained by the White and Cheyenne Rivers. The flora of these canyons was studied in 1939 and 1940.

Cherry County is 150 miles west of the transition between the true and mixed prairies. Pine Ridge is in the heart of the mixed prairie 150 miles west of Valentine in eastern Cherry County.

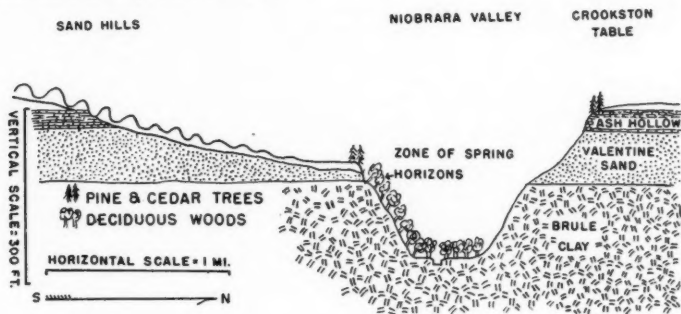
The average annual precipitation at Valentine for a period of 51 years was 18.3 inches; and that at Chadron in Pine Ridge was the same during a period of 26 years.

The summer climate of this semiarid region is characterized by a growing season of moderate length, with occasional thundershowers, high daily temperatures, relatively cool nights, low relative humidities, high rates of evaporation, and prevailing south winds. The average frost-free period is 151 days at Valentine, and 144 days at Chadron.

The winters are moderately cold, with minimum temperatures as low as  $-10^{\circ}$  to  $-38^{\circ}$ . Snowfall is light and of little value in restoration of moisture on the table-lands and wind-swept tops of sand dunes. Much of the snow is blown into low, protected places or to the leeward side of steep slopes along the edges of table-lands. Prevailing winds in winter are from the west and northwest.

## PHYSICAL FEATURES OF HABITATS WITH RARE PLANTS

The geological and topographical features of the valley habitats 10 miles east of Valentine are shown in Fig. 2. Here the Niobrara River prior to the close of Wisconsin glaciation eroded away the limy and sandy formations on the surface. A broad valley was formed, but during post-Wisconsin time the Niobrara River renewed erosion and cut a deep, narrow canyon into the Brule clay along the north edge of the old valley. Simultaneously this gave rise to the Valentine terrace. As this took place the sands of the terrace were worked into sand hills by wind erosion.



Large quantities of rain are absorbed directly by the sand hills south of the present-day valley, and as a result, a large quantity of ground water accumulates in the sands above the impervious Brule clay. This ground water is drained at the Niobrara Valley where the top of the clay is exposed 75 to 100 feet above the river. Water from numerous springs and seepages runs down the hillsides in small streams, and a large part of the north slope is subirrigated. The flow is constant throughout the year, and the water at spring horizons remains at a temperature of  $54^{\circ}$  F. through all the seasons. The mesic vegetation on these slopes not only receives an abundance of natural irrigation, but also is protected from the prevailing south winds of summer and direct radiation of the sun. These slopes are covered with deciduous woods.

On the Crookston Table the surface formation (Ash Hollow) gives rise to fine sandy loam soils, and therefore rain is not absorbed in sufficient quantity to form a high water table above the Brule clay nor to maintain a large number of springs on the valley slopes where the clay formation is exposed. Runoff has eroded deep canyons into the Crookston Table for a distance of several miles north from the Niobrara River. Thus the north slopes of the Niobrara Valley are without irrigation; they also receive direct rays of the sun and the full impact of the prevailing south winds of summer. They are covered with mixed-prairie grasses.

The canyons in Pine Ridge are not as well irrigated as the south slopes

of the Niobrara Valley, and the lands immediately along the small streams are occasionally flooded. Some areas, however, have seepage and spring water, and most of the mesophytic habitats receive a limited amount of run-in water from rock exposures. Snow is also blown in from higher levels. The deep canyons are protected from the prevailing south and west winds. Elevations are nearly 4,000 feet, sufficient to cause cooler temperatures than are characteristic of the Niobrara Valley in Cherry County where elevations approximate 2,500 feet.

The habitats in the sand hills which have permitted survival of rare plants are usually located near springs. These commonly occur near the heads of drainages or along the permanent streams where there is little flooding. Sometimes they are a few feet above nearby lakes which have a relatively stable water level. Drainage of these habitats is sufficiently constant throughout the year to prevent desiccation by lowering of the water level during periods of drouth. Stability of these environments has permitted survival of a mesophytic flora in a semi-arid climate.

#### RARE PLANTS

Many tall grasses, trees, shrubs and associated forbs are not included in the category of rare plants because they are very common locally and have nearly a continuous distribution. They are regarded as postclimax species. They are very mobile and well adapted to their environments. The rare plants, however, were found at widely separated stations, and occurred only in the most favorable and stable habitats.

Table 1 lists the rare, mesophytic species which were found in deciduous woodlands in the Niobrara Valley in Cherry County and in the canyons of Pine Ridge. Altogether 92 rare ferns and flowering plants were collected. Forty rare species were recorded as common to both areas; 30 were found only in the Niobrara Valley and 22 were found only in the canyons of Pine Ridge.

Rare plants in the sand hills occur in tall-grass meadows and at springs. Those which grow in shallow water or on tussocks are *Carex comosa* Boott., *C. lacustris* Willd., *C. hystricina* Muhl., *C. diandra* Shrank., *C. substricta* (Kukenth.) Mackenzie, *Glyceria grandis* S. Wats., *Ranunculus delphinifolius* Torr., *Lysimachia thyrsiflora* L., *Menyanthes trifoliata* L., and *Utricularia minor* L.

Aquatic plants which occur mostly on the shores of small, spring-fed streams include *Acorus Calamus* L. *Mimulus glabratus* *Fremontii* (Benth.) Grant, *Berula erecta* (Huds.) Coville, *Catabrosa aquatica* (L.) Beauv., *Calamagrostis canadensis* (Michx.) Beauv., *Mentha piperita* L., and *Veronica americana* Schwein.

Areas of peaty soils where the water table is relatively constant and close to the surface were dominated by *Salix petiolaris* Smith and *Thelypteris palustris* Schott. Plants of special interest in this community were *Doellingeria umbellata* (Mill.) Nees., *Tridenum virginicum* (L.) Raf., *Gentiana Andrewsii*

TABLE 1.—A list of rare plants in deciduous woodlands in the canyons of Pine Ridge and in the Niobrara Valley in Cherry County.

Plants found both in Pine Ridge and Niobrara Valley	herbs	<i>Woodсия oregana</i> D. C. Eat. <i>Botrychium virginianum</i> (L.) Sw. <i>Carex Sprengelii</i> Dewey <i>C. saximontana</i> Mackenzie <i>C. blanda</i> Dewey <i>Oryzopsis micrantha</i> (Trin. & Rupr.) Thurb. <i>Poa interior</i> Rydb. <i>P. sylvestris</i> A. Gray <i>Bromus latiglumis</i> Hitchc. <i>Smilax lasioneuron</i> Hook. <i>Polygonatum commutatum</i> (Schultes) Dietr. <i>Smilacina stellata</i> (L.) Desf. <i>Habenaria bracteata</i> (Willd.) R. Br. <i>Silene Menziesii</i> Hook. <i>Ranunculus abortivus</i> L.	<i>Aquilegia canadensis</i> L. <i>Heuchera Richardsonii</i> R. Br. <i>Fragaria americana</i> (Porter) Britt. <i>Geum canadense</i> Jacq. <i>Viola canadensis</i> L. <i>Circaea lutetiana</i> L. <i>Heracleum lanatum</i> Michx. <i>Osmorrhiza longistylis</i> (Torr.) DC. <i>Sanicula canadensis</i> L. <i>Pyrola chlorantha</i> Sw. <i>Phryma leptostachya</i> L. <i>Monarda mollis</i> L. <i>Collinsia parviflora</i> Dougl. <i>Galium triflorum</i> Michx. <i>Erigeron philadelphicus</i> L. <i>Rudbeckia hirta</i> L. <i>Eupatorium maculatum</i> L.
	woody plants	<i>Juniperus horizontalis</i> Moench <i>Populus tremuloides</i> Michx. <i>Ribes setosa</i> Lindl. <i>Ribes americana</i> Mill.	<i>Crataegus succulenta</i> Schrad. <i>Amelanchier alnifolia</i> Nutt. <i>Rubus occidentalis</i> L. <i>Symphoricarpos albus</i> (L.) Blake
Plants found only in Niobrara Valley	herbs	<i>Filix bulbifera</i> (L.) Underw. <i>Thelypteris palustris</i> Schott. <i>Carex eburnea</i> Boott. <i>C. Peckii</i> Howe. <i>Cinna arundinacea</i> L. <i>Festuca obtusa</i> Spreng. <i>Laportea canadensis</i> (L.) Gaud. <i>Corydalis montana</i> Engelm. <i>Desmodium acuminatum</i> (Michx.) DC. <i>Apios americana</i> Med.	<i>Amphicarpa bracteata</i> (L.) Fernald <i>Arenaria lateriflora</i> L. <i>Impatiens pallida</i> Nutt. <i>Pterospora Andromedea</i> Nutt. <i>Gentiana Andrewsii</i> Griseb. <i>Lappula virginiana</i> (L.) Greene <i>Campanula americana</i> L. <i>Solidago speciosa</i> Nutt. <i>Erigeron flagellaris</i> A. Gray
	woody plants	<i>Salix petiolaris</i> Smith <i>Juglans nigra</i> L. <i>Betula papyrifera</i> Marsh <i>Ostrya virginiana</i> (Mill.) K. Koch. <i>Corylus americana</i> Walt.	<i>Physocarpa intermedia</i> (Rydb.) K. C. <i>Rhamnus lanceolata</i> Pursh [Schneider] <i>Zanthoxylum americanus</i> Mill. <i>Tilia americana</i> L. <i>Lonicera glaucescens</i> Rydb. <i>Aralia nudicaulis</i> L.
Plants found only in Pine Ridge	herbs	<i>Scirpus microcarpus</i> Presl. <i>Carex grisea</i> Wahl. <i>C. aenea</i> Fernald <i>C. vulpinoidea</i> Michx. <i>Poa ampla</i> Merr <i>P. glaucifolia</i> Scribn. & Williams <i>Schizachne purpurascens</i> (Torr.) Swallen	<i>Fritillaria atropurpurea</i> Nutt. <i>Actaea alba</i> (L.) Mill. <i>A. rubra</i> (Ait.) Willd. <i>Thalictrum venulosum</i> Trelease <i>Penstemon glaber</i> Pursh <i>Antennaria obovata</i> E. Nels.
	woody plants	<i>Juniperus communis</i> L. <i>Salix Bebbiana</i> Sarg. <i>Betula fontinalis</i> Sarg. <i>Ribes inebrians</i> Lindl. <i>Prunus virginiana</i> L.	<i>Amelanchier canadensis</i> (L.) Medic. <i>Mahonia Aquifolium</i> (Pursh) Nutt. <i>Acer glabrum</i> Torr. <i>Cercocarpus montanus</i> Raf.

(Griseb.) Small, *Onoclea sensibilis* L., *Galium trifidum* L., *Scutellaria epilobifolia* A. Hamilt., *Campanula aparinoides* Pursh, and *Pilea pumila* (L.) A. Gray. *Cyperus Engelmanni* Steud., *Juncus marginatus* Rostk., and *J. nodosus* L. occur occasionally on sandy shores of ponds and streams.

Unusual plants which were recorded in tall-grass meadows include *Cypripedium candidum* Muhl., *Spiranthes cernua* (L.) Richard., *Habenaria leucophaea* Nutt., *Sisyrinchium angustifolium* Mill., *Hypoxis hirsuta* (L.) Coville, *Lilium umbellatum* Pursh, *Agrostis exarata* Trin., *Fimbristylis interior* Britton, *Carex aurea* Nutt., *C. Crawei* Dewey, *Juncus longistylis* Torr., *Geum strictum* Soland., *Agrimonia striata* Michx., *Campanula rotundifolia* L., and *Lobelia spicata* Lam.

*Eriophorum angustifolium* Roth., *E. gracile* Koch., *E. virginicum* L., *Caltha palustris* L., and *Ophioglossum vulgatum* L., recorded by early collectors, were not found in this study.

The rare plants in Cherry County and in Pine Ridge are on the border of their range. Certain Rocky Mountain species are on the eastern edge of their range, and certain characteristic plants of the deciduous forest are on their western border. Some are widely distributed in both the Rocky Mountains, the deciduous forest, and in Canada. The nearest records of *Betula papyrifera* are in the Black Hills and eastern Minnesota, some 200 to 400 miles distant. *Symphoricarpos albus* is recorded from both Pine Ridge and Cherry County. Closest records of these are in the Black Hills and northern Minnesota (Jones 1940). *Desmodium acuminatum* is confined to the deciduous forest and occurs in the woods of eastern Nebraska. *Juglans nigra* and *Tilia americana* are on the most northwest limits of their range. *Collinsia parviflora* and *Silene Menziesii* are on the extreme eastern limits of their distribution. Records of *Ophioglossum vulgatum* is of special interest because it occurs nearly 1000 miles west of its major distribution (Clausen 1938). *Carex Peckii* and *C. eburnea* have their major range north and northeast of Nebraska.

The rare plants in the deciduous woods represent outposts of species of three geographical areas; the deciduous, the montane, and the boreal forests. Those at springs and in the tall-grass meadows have their major distribution in the east and north. There are few rare plants with their major distribution in the southern great plains and prairies.

#### SUMMARY

Many mesophytic habitats in the sand hills and in the canyons of Pine Ridge and the Niobrara Valley in northern Nebraska result from the interrelations of geology, soils, topography and ground water. Altogether 141 unusual plants are recorded from these habitats. Ten were found in swampy habitats, and the same number both along the shores of small streams and in peaty soils. Fourteen were collected in the tall-grass meadows. The greatest number of rare plants occurred in the deciduous woods where a total of 92 were found. Five unusual plants that were reported formerly, were not found during this study.

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## New and Noteworthy Records of the Flora of Nebraska

W. L. Tolstead

This paper deals with new records for the state of Nebraska and extension of range of several plants along with notes on habitat or other things of interest. All species are represented by specimens in the Herbarium at the University of Nebraska and at other herbaria as indicated. The collection numbers are enclosed in parentheses; all are the author's except as otherwise indicated.

Certain grasses have been identified by Jason R. Swallen. *Poa trivialis* L., *P. canbyi* (Scribn.) Piper, and *P. Fendleriana* Steud. are new records for Nebraska. *Poa canbyi* is common in the mixed prairie in Pine Ridge where it has increased considerably during the past period of drought. *Poa Fendleriana* was found in Dawes County in Indian Canyon (11) and in Sioux County on the Piper Ranch (17) where it grew on protected slopes covered with open stands of ponderosa pine. *Poa trivialis* grows in large quantities along small streams in Pine Ridge (6). *Poa glaucifolia* Scribn. & Williams (*Poa plattensis* Rydb.) was found in open woods of pine in Dawes County (12), and in Franklin County (41683) in protected ravines. *Poa sylvestris* Gray, formerly recorded by Bates from Long Pine, was found in swampy land at Valentine, Cherry County (10) and at Chadron State Park, Dawes County (9).

A few specimens of *Glyceria borealis* (Nash) Hitchc. (41646) were found in the Valentine Lakes Refuge in Cherry County. It grew on the shores of a small pond. *Leptoloma cognatum* (Schult.) Chase (41715) was collected in a thicket of choke cherry and plum in the sand hills along Thompson Creek in Franklin County. This is the first time it has been collected in the sand-hill habitats of Nebraska.

*Schizachne purpurascens* (Torr.) Swallen was found in a slightly grazed pasture in Bordeaux Valley in Dawes County. *Bromus japonicus* Thurb. (5), which was first introduced into western Nebraska early in this century, has become very common, especially in disturbed areas on the mixed prairie. So far as is known *Bromus pumpellianus* Scribn. and *B. anomalus* Rupr. (1 and 2 respectively) are new records for Nebraska. They grow in Pine Ridge on protected slopes covered with open stands of pine.

*Carex Hallii* Olney was found in wet meadows at Kingsley Dam in Keith County (41359) and in Dundy County (41361). This species heretofore has been referred to *C. Parryana* Dewey in some Nebraska collections.

While collecting with Howard C. Reynolds in Richardson County, three species of *Carex* were collected which are new records for the state. These include *Carex Jamesii* Schwein. (H. C. Reynolds 1450), *C. conjuncta* Boott (H.



*C. Reynolds* 1490), and *C. festucea* Schk. (*H. C. Reynolds* 1517). These three species of *Carex* were identified by F. J. Hermann.

Specimens of *Scirpus saximontanus* Fernald have been identified by Allan A. Beetle. The few specimens formerly collected in Nebraska have been referred to *S. Hallii* A. Gray. This annual rush was found in depressions on the Loess Plain in Franklin (41424), Fillmore (41425), Perkins (41426), northeast corner of Harlan (41427) and Clay (41432) counties. *Scirpus heterochaetus* Chase (4162) was found in a temporary pond on the Loess Plain in Fillmore Co. 2 miles northwest of Shickley.

*Eleocharis atropurpurea* (Retz.) Kunth. was collected on shores of a temporary pond in Perkins County (41184) and in Franklin Co. near Macon (41187). This has been reported from Nebraska by H. K. Svenson, but no specimens were in the Nebraska herbarium until these collections were added. *Eleocharis rostellata* Torr. is recorded from Nebraska for the first time. It was abundant in Dundy County, especially on subirrigated slopes where the Ash Hollow limy sandstone is near the surface but covered with a few feet of sand. It was found 6 miles north of Haigler (41188) and 1 mile north of Rock Creek Fish Hatchery (41190) in Dundy County, at McGuire's Slough (41191) in Chase County, and grew along shores of ponds in the Republican Valley in Hitchcock (41194) and Harlan (41196) counties. *Eleocharis Engelmanni* Steud. heretofore has been reported from a few stations in Nebraska, but collections in 1941 revealed that it is widely distributed in small, temporary ponds, and it is very common locally. Specimens were collected in Perkins (41206) and Sheridan (41204) counties on the High Plains and in eleven counties on the Loess Plain: Clay (41197), Webster (41200), Fillmore (41201), Franklin (41202), Thayer (41205), Phelps (41208), Saline (41209), Harlan (41211), Hamilton (41212), Kearney (41213), and Nuckolls (41824). In addition it was collected in Holt County (41210) in the sand hills and on the flood plain of Salt Creek near Lincoln in Lancaster County. Identifications were verified by H. K. Svenson and specimens were deposited in the Herbarium of the Brooklyn Botanical Garden and the Missouri Botanical Garden.

*Potamogeton dimorphus* Raf. was rediscovered in Nebraska in a large, temporary pond on the Loess Plain in Fillmore County, 2 miles northwest of Shickley. *Potamogeton strictifolius* A. Benn. (477), which has been referred to other species in Nebraska collections, was identified by E. C. Ogden. It is a common pioneer in fresh-water ponds throughout the western part of the state. During 1941 it was collected in Dundy (41501), Hall (41502), and Webster (41504) counties.

*Nothoscordum bivalve* (L.) Britton (41488) was found in a broad ravine in Pawnee County near Table Rock. It grew among tall grasses.

*Salix exigua* var. *luteosericea* (Rydb.) Schn. (548) occurs occasionally in the meadows of the sand hills in Cherry County. It has not been recorded in Nebraska heretofore so far as is known to the author. Specimens were identified by C. R. Ball.

The range of *Larrea Jamesii* (T. & G.) Britt (411026, 411027) is extended into Nebraska by specimens found in two localities on fine sands in Chase County.

*Croton monanthogynus* Michx. (411279) and *Tragia stylaris* Muell. Arg. (411215) grew on rock outcrops of limy sandstone at Lookout Mountain in Franklin County. These were identified by Louis C. Wheeler.

A single plant of *Limosella aquatica* L. was found on shores of a small pond near Grant in Perkins County. It is recorded from Deuel and Scotts Bluff counties in Pennell's monograph on the Scrophulariaceae, but it occurs very rarely in Nebraska.

*Linaria texana* Scheele (134), which is recorded from Halsey by Pennell, was collected in a dry meadow in the Valentine Lakes Refuge in Cherry County. The specimens were identified by F. W. Pennell.

*Proboscidea louisiana* (Nutt.) Woot. & Standl. appears to be new to the state. It was found in a few places in the Republican Valley where it is a pioneer on sands and mud flats along the river and on the shores of small ponds. It was recorded from Red Willow County (411121), Furnas County south of Beaver City (411122) and Franklin County along Thompson Creek (411123).

*Utricularia minor* L. (411120) occurs in a large swamp in Spring Creek Valley in Chase County. It grew in shallow water between plants of *Typha*. It has been recorded from Thedford.

The range of *Ruellia ciliosa* Pursh (411119) has been extended westward into Jefferson County where it grew in burr oak woods south of Fairbury.

*Lobelia cardinalis* L. has been recorded from Franklin County. In the summer of 1941, however, it was collected at springs in the Republican Valley in Franklin (411062), Webster (411063), Dundy (411065), and Hitchcock (411066) counties.

Several species of Compositae have been identified by Dr. S. F. Blake. Specimens are deposited in the National Arboretum at Washington, D. C. *Solidago speciosa angustata* T. & G. (771, 411530) occurs only at spring horizons at Fort Niobrara and Smiths Falls in Cherry County. *Senecio tridenticulatus* Rydb. was collected in a blowout in Holt County (75). *Erigeron nematophyllus* Rydb. (28) was found on rock outcrops on the edge of the Harrison Table in Sioux County. It has not been collected formerly because it flowers and seeds before June first. *Aster laevis Geyeri* Gray is common in woodlands throughout the Niobrara Valley and in the canyons of Pine Ridge (803, 402).

Several species of semi-aquatic plants grow in temporary ponds in the mixed prairie region. Since these ponds are dry in periods of drought, their flora has been collected very little. The year 1941 was favorable for growth of such plants and they were found in a number of places on the Loess and High Plains of Nebraska.

*Heteranthera limosa* (Sw.) Willd. has been collected very little in Nebraska but in 1941 it was found in five counties on the Loess Plain: Hamilton (41490), Clay (41491), Nuckolls (41492), Webster (41493), Fillmore (41496) counties. The same is true of *Lophotocarpus calycinus* (Engelm.) J. G. Smith. Plants were found in Perkins (41411) and Sheridan (41420) counties and six counties on the Loess Plain: Fillmore (41413), Clay (41414), Hamilton (41415), Kearney (41417), Phelps (41418), and Franklin (41419). *Marsilia vestita* Hook. & Grev. grows in quantity in small, muddy ponds, some of which last only a few weeks in early summer. Specimens were collected in Chase (41570), Perkins (41572), Sheridan (41577), and Box Butte (41578) counties on the High Plains, and in Hayes (41569), Franklin (41572), Kearney (4157), Dundy (41573), Fillmore (41574), and Harlan (41576) counties on the Loess Plain. *Isoetes melanopoda* J. Gay was collected in 5 counties on the Loess Plain: Fillmore (41579), Clay (41581), Kearney (41582), Hamilton (41583), and Harlan (41584) counties. *Didiplis diandra* (Nutt.) Wood, which grows prostrate upon muddy shores of ponds, was found in Perkins (411216), Hamilton (411218), and Kearney (411220) counties. It has been recorded only from Lincoln to date.

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# **Vegetational Correlations with Vapor Pressure Deficit and Relative Humidity<sup>1</sup>**

Carl B. Huffaker

## **Introduction**

Ecologists have long attempted to single out critical environmental factors for use in distributional, successional, and other ecological studies. Temperature and relative humidity have been foremost in consideration. In recent years the importance of relative humidity, and even of temperature, has been minimized. The evaporating power of the air is looked upon as a far more critical factor for plants. The paucity of evaporation records and the lack of widely acceptable methods for measuring evaporation have prompted the consideration of factors which can be used in lieu of atmospheric evaporating power.

The steepness of the diffusion vapor pressure gradient is of primary importance in evaporation. Water diffuses rapidly from a region of high vapor pressure (as next to a water surface) to one of low. It diffuses progressively more slowly to regions of higher vapor pressure. A high relative humidity makes for a high water vapor pressure, so that the diffusion gradient is partially a function of relative humidity. Wind is a factor which is concerned, fundamentally, with this steepness of the diffusion gradient. Air currents remove the layers of moist air over the evaporating surface, substituting drier air, so that the distance between an area of relative saturation and one of a greater moisture deficiency is less. Leighly (1937) advanced a theory of evaporation into moving air based upon the diffusion of water molecules through a laminar boundary of air next to the evaporation surfaces, the thickness of this laminar layer decreasing with the increase in wind velocity. The speed of water molecules, and consequently the diffusion pressure created, is also greatly increased by temperature. Day (1917) and Anderson (1936) wrote that the pressure of water vapor is approximately doubled for every increase in temperature of 20° F. Where the relative humidity is the same, water vapor will move in volume from the point of higher temperature to that of the lower.

It is, therefore, not surprising that Szymkiewicz (1927), Braun-Blanquet (1932:135), Anderson (1936), Livingston and Shreve (1921:287) and others have reached conclusions which indicate that relative humidity alone is of little or no significance as an index of evaporation. The latter authors stated that relative humidity bears no quantitative relation to the evaporating power of

<sup>1</sup> This paper is a revision from a thesis submitted to the Committee on Graduate Study of the University of Tennessee in partial fulfillment of the degree of Master of Science. Contribution from the Botanical Laboratory, The University of Tennessee. New. Ser. No. 52.

air. On the other hand, they stated that the evaporation rate is determined by the difference between the maximum and the actual (i.e. — the vapor pressure deficit — hereinafter referred to as v.p.d.) rather than by the percentage of the maximum vapor pressure possible at the temperature. They further stated that, disregarding wind velocity and when the air and evaporation surface temperatures are equal, evaporation should be proportional to the v.p.d. Johnston (1919) found a better correlation between evaporation and v.p.d. than between evaporation and relative humidity, when wind velocity was taken into account.

Turnage and Shreve (1939) held to the view that v.p.d., relative humidity, the temperature of the dew-point and wet-bulb depression all have advantages; but concluded, "The best correlation is obtained between evaporation and wet-bulb depression, the relation being linear for any given velocity." Leighly (1937) also inferred that wet-bulb depression should be a better indicator of evaporation than v.p.d., particularly where the evaporation is from surfaces like porous-cup evaporimeters, since such a surface would have a temperature nearer that of the wet-bulb than the dry-bulb. However, the temperature of transpiring leaf surfaces of mesophytic plants is probably closer to that of the dry-bulb than the wet-bulb, which would speak in favor of v.p.d. over wet-bulb depression as an indication of evaporation for use in plant ecology. Curtis (1938) concluded that, "To lower the temperature of a leaf below that of the air when the leaf is in direct sunlight would seem to require impossibly high transpiration rates." There is, therefore, considerable evidence that plant evaporating surfaces average approximately the same as atmospheric temperatures. Hence, Thornthwaite's (1940) criticisms of v.p.d., though valid in a strict sense, do not represent a serious objection to the use of v.p.d. data in broad correlations. The impracticality of making temperature readings of evaporation surfaces does not justify the abandonment of v.p.d. data. Such temperature measurements are difficult in physiological studies and impossible for broad ecological and plant geographic work.

It is through transpiration that the evaporating power of the air, and hence v.p.d. or any other atmospheric moisture factors, takes its significance in plant ecological studies. It is certainly true that transpiration and evaporation from free-water surfaces, or even from evaporimeter surfaces, do not vary in an identical way. Under special conditions, or in nature, they may differ considerably. Yet, many interesting and fundamentally true correlations of vegetation with climate have been found by the use of atmometers on every continent and in every climatic zone. In any consideration of evaporation it must be borne in mind that transpiration is affected by (1) insolation, (2) atmospheric evaporating power and (3) internal conditions of the plant.

There are innumerable instances in biogeographical literature of broad correlations with climatic factors. The circumpolar coniferous forest formation (*Aciculilignosa* of Rübél) is bounded on the north directly by a temperature relation. The regions farther northward are so cold that the soil remains frozen in the layer where the tree roots absorb and the indirect limiting factor is seen to be one of soil dryness. The tundra (*Frigiorideserta* of Rübél) farther north

is able to utilize the free water present during the very short growing season in the unfrozen upper layer of the soil.

Livingston and Shreve (1921:583) wrote, "With respect to the generalized vegetation areas of the United States, one of the most clear-cut evidences of a fundamental correlation exists in the correspondence between the position of the vegetational boundaries and the position of the isoclimatic lines expressing certain values of the moisture ratio (precipitation/evaporation ratio) for the average frostless season." Transeau (1905) had previously found similar evidence of correlation. The former authors (1921:27) stated, "It is quite true that the water-relations of plants have more to do with the control of the local and general distribution of vegetation than have any other conditions. This is not true of the local and general distribution of the species themselves, for we here find temperature relations playing a strong rôle."

Szymkiewicz (1923-1927) favored v.p.d. expressions as being superior to measurement of evaporation by evaporimeters. He found close correlations between v.p.d. and vegetation in Europe.

Phytogeographic correlations with climatic factors may become very complicated through the interaction of both atmospheric and edaphic factors upon the organisms concerned. Jenny (1930) stated that along both the 11° and 19° C. annual isotherms, "the average nitrogen content of grassland soils increases logarithmically with humidity factors (precipitation/v.p.d.) while the nitrogen content of subtropical timber soils is not influenced by humidity factors." This is one of the many cases where atmospheric factors may account for the prevailing edaphic conditions of a region.

Merriam's (1894) unprecedented attempt to define broadly American biotic zones in terms of climate at first met with great approval, and certainly he deserves credit for his pioneer undertaking. As the facts of biotic distribution have been worked out piece-meal, his work has found increasing disapproval, until it is now generally accepted that his major conclusions were unwarranted, and that his life zones sometimes run contrawise to the major biomes.

This paper is an attempt to test the value of v.p.d. as an ecological factor, by studying the correlations between vegetational distributions and that factor. These correlations are compared with relative humidity correlations for the same distributions.

#### Methods and Procedure in the Preparation of Illustrations

The relative humidity and temperature data which are the basis of the various illustrations presented in this paper were copied from "Climatological Data for the United States by Sections," published by the U.S.D.A., Weather Bureau.

The values of v.p.d. and relative humidity presented are mostly means at noon, or somewhat later, for the 10-year period, 1928-1937. Data are from all stations (187) reporting noon relative humidity for four or more of these ten

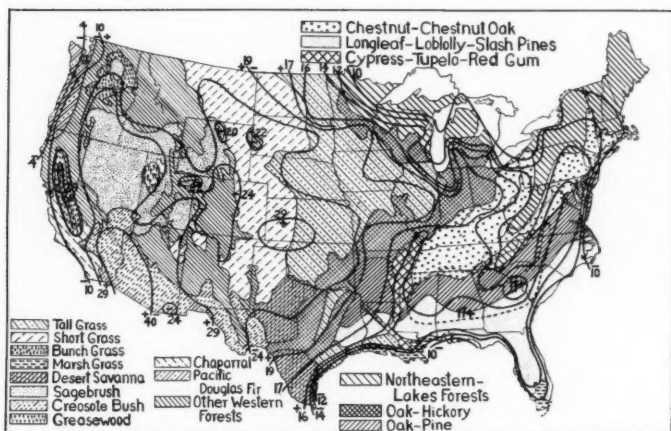


Fig. 1. Isoclimatic Lines of Vapor Pressure Deficits and Vegetation Areas. Vegetation Modified from Shantz and Zon (1923).

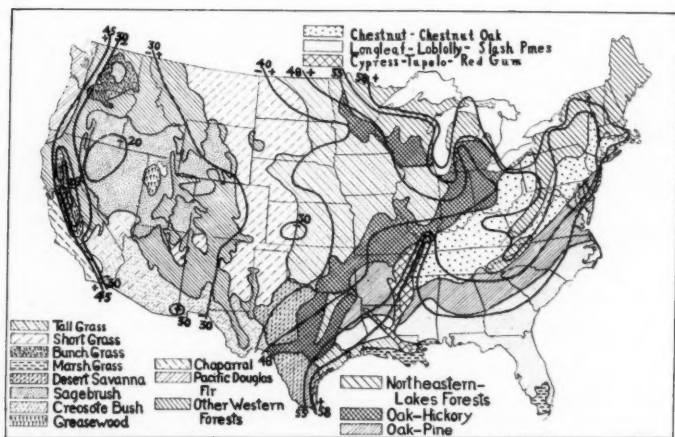


Fig. 2. Isoclimatic Lines of Relative Humidities and Vegetation Areas. Vegetation Modified from Shantz and Zon (1923).



years. Noon temperatures were not available. Daily maxima had to be used instead. It is assumed that v.p.d. values calculated from the maximum temperatures and noon relative humidities are not far different from the v.p.d. values at the time of highest transpiration.

Average v.p.d. values for the 10-year period were calculated for each month for each of the stations. It was first necessary to prepare a v.p.d. table by 1 per cent relative humidity and 1° C. temperature intervals.

The v.p.d. (or relative humidity value as the case may be) for a particular month for each station was marked on large-scale county outline maps. Lines were then drawn between points of equal v.p.d. (or equal relative humidity). Simple arithmetic interpolation was used between stations. If there were any station records which indicated a deviation from the general trend of a line, to include or exclude certain mountainous or other topographic units, this was done. In the region of the Rocky Mountains and the Southern Appalachian Mountains this interpretation was characteristic.

Maps for both relative humidities and v.p.d. values for several diversified months were prepared, but those for July alone seemed worth presentation. Annual v.p.d. and relative humidity complement curves for the major vegetation types were also prepared.

The isoclimatic lines were then drawn over a base vegetation map which is a modification from the map of Shantz and Zon (1924). It was considered the most accurate and detailed map available for this purpose. In the main, the divisions of all the major extensive vegetation types were maintained, the only exception being a grouping of all western forests except Douglas fir and chaparral into a single heterogeneous group.

### Correlations between V.P.D. and Natural Vegetation

#### EASTERN VEGETATION

Figure 1 shows lines of equal v.p.d. values for July superimposed upon natural vegetation areas, with the exception that the dotted line in the southeastern United States indicates a 17-mm. v.p.d. line for the "driest month" of the year. By the "driest month" is meant that month of the year having the highest v.p.d. for each station independently.

The v.p.d. line of 17 mm. for July roughly divides the United States into two atmospheric moisture regions, disregarding coastal areas for the moment. The small isolated area of 17 mm. in South Carolina and Georgia is the only one having a higher v.p.d. value for July east of this general 17-mm. line, which roughly parallels the extreme eastern boundary of oak-hickory. This is a relative measure of the more mesic vegetation of the eastern United States in general, since all the continental areas west of this line have higher v.p.d. values.

A lower v.p.d. than 14 mm. is found only on the coasts of the South, East, and West (oceanic influences), along the Great Lakes and the New England states, and in the southern Appalachian Range. It is likely, however, that if

records were available for sufficiently high altitudes, even in the Rocky Mountains, lower values than 14 mm. would be found. It is thus assumed that the minimal v.p.d. lines of the western mountains are actually much lower than indicated in Figure 1.

The 19-mm. line exhibits a trend which in its extreme eastern limit remarkably coincides with the eastern boundary of tall grassland and with the western boundary of oak-hickory at the same position. The line bears much too far southwest into the center of Iowa to serve as a boundary for oak-hickory in that area, however. A probable explanation is that oak-hickory here predominates along the river valleys and records for the region are from stations located in oak-hickory river valleys rather than in the general upland tall grassland prairies. The general directions of this line in the north, south, and center compare to the boundary between oak-hickory and tall grassland.

The major portions of chestnut-chestnut oak, longleaf-loblolly slash pines, and oak-pine are found in regions of v.p.d. lower than 17 mm. and higher than 14 mm. The presence of cypress-tupelo-red gum (an edaphic type) along the Lower Mississippi Valley serves to separate the oak-pine region into two parts. A small part of the isolated area of oak-pine west of the Mississippi also has a v.p.d. below 17 mm. The rest lies between the 17-mm. and 19-mm. lines, which is a range typified by considerable variability and transition from the more mesic forests of the Eastern United States to the grasslands of the Central Plains. The same general account holds for longleaf-loblolly-slash pines areas, except that in this case the major portion lies south of the 16-mm. line. Oak-pine and chestnut-chestnut oak collectively are bounded on the west and south by 17-mm. and 16-mm. lines, respectively, and along the Appalachian Range and in the north by a 14-mm. line. In order to differentiate between oak-hickory and chestnut-chestnut oak on the basis of v.p.d. lines, it was necessary to draw the dotted 17-mm. line in Figure 1, representing v.p.d. values for the driest month. This area has the highest v.p.d. values of any region in the Eastern United States. Also, considering the data (not illustrated here) for the driest month alone, it was found that the chestnut-chestnut oak and longleaf-loblolly-slash pine types were indistinguishable on the basis of v.p.d. The oak-pine type between these two is represented by a region of high v.p.d. range, due to low relative humidity values and high temperatures. A lower v.p.d. is found in the longleaf-loblolly-slash pine region as a result of the high relative humidity (coastal effect), although temperatures are also high. A lower v.p.d. in chestnut-chestnut oak, however, results from lower temperatures rather than high relative humidities. It is seen that these types have their driest months at different times of the year, for in July the two fall within different v.p.d. groups. In chestnut-chestnut oak, July is the driest month, but June is driest in longleaf-loblolly-slash pines.

Dice's (1938) Canadian province is essentially the same as the region designated by Nichols (1935) as hemlock-white pine-northern hardwood forest, except in one principal consideration. Dice terminates his province at the southern border of Pennsylvania after only a minor extension southward in

the region of the Appalachian Mountains. On the other hand, Nichols' area is extended southward to include the Southern Appalachian Mountains. Not only are the characteristic species of his Canadian province found farther south, but such species form the dominant vegetation of large sections in the Southern Appalachian Mountains, as shown by the presence of spruce (*Picea*), fir (*Abies*), birch (*Betula*), beech (*Fagus*), and maple (*Acer*), as indicated by Shantz and Zon (1924). Shantz and Zon's northeastern hardwoods region taken together with his spruce-fir and northeastern pine forest present a definite Southern Appalachian extension which is in close conformity with that of Nichols. This union of hardwoods and conifers in the Southern Appalachian region was used in the base map of Figures 1 and 2.

The presence of an affinity with respect to v.p.d. for July between the Southern Appalachians and the Canadian, or northern hardwoods, region lends support both to v.p.d. as a critical ecological factor and to the extension of the province southward to include the Southern Appalachians. The 14-mm. v.p.d. line for July corresponds in a general way with the southern boundary of the northeastern-lakes forest combination type as included in the present vegetation map. This region has the same general southern boundary as that presented by Nichols (1935) for his northern hardwoods.

#### WESTERN VEGETATION

As revealed in Figure 1, tall grassland has an eastern limit which agrees with the 19-mm. v.p.d. line for July. The extension eastward into Illinois is also closely correlated with this isocline. The westward protrusions in Nebraska and South Dakota are closely paralleled by the 24-mm. line at those positions. The southern portion of tall grassland in Texas, Oklahoma and Kansas lies between the 24- and 29-mm. lines. Hence, this portion of tall grassland falls within the general v.p.d. range of short grassland, and v.p.d. does not adequately divide the two vegetation types throughout the Central Plains. However, even in this instance the v.p.d. correlations with actual evaporation are good. Livingston and Shreve (1921:324) presented a map of average 5-week evaporation values for the summer of 1908. From this map it can be seen that both a southern (300 cu. cm.) line and a northern (150 cu. cm.) line cross the plains grassland in question, as do the v.p.d. lines of Figure 1. A 26-mm. v.p.d. line (not shown) crosses the plains grassland in the south, similarly as does the 300-cu.cm. line for evaporation.

The isolated area having v.p.d. values of over 29 mm. in Kansas embraces both tall grassland and short grassland, although it would be expected on the basis of v.p.d. to support semi-desert vegetation. The record for stations in Kansas is only from 1933 to 1937. It is possible that the vegetation here is more xeric or becoming more xeric than the typical vegetation of short and tall grassland, or that the record is for weather rather than mean climate.

The arid island of bunch grass in California is well correlated with the region of v.p.d. above 29 mm. In the northern region of the same type, in Washington and Oregon, both the 29- and 24-mm. lines bear northward,

revealing that it has an affinity with the more arid conditions. As with the plains grassland, the lower temperatures in the north have produced a lower v.p.d. for the area than would be expected if this factor is to be considered critical with regard to this vegetation. On the other hand, Shreve (Livingston and Shreve, 1921) considered the southern tip of this region with the sagebrush vegetation of the Great Basin, an arrangement well in accord with the v.p.d. lines as here shown. He considered the rest of the northern bunch grass type, as here treated, grassland. A good portion of it has a v.p.d. of from 24 to 29 mm., which represents the general v.p.d. range of short grassland.

Creosote bush and sagebrush types occur almost completely within regions of over 29 mm. v.p.d. One exception to this situation is found in the creosote bush area in Western Texas. Furthermore, sagebrush is found primarily where v.p.d. values of 29 to 40 mm. prevail, with creosote bush (the most xerophytic type) occurring in the most arid region—the California and Arizona region having v.p.d. values above 40 mm.

In the Northwest, the eastern boundary of the Pacific Douglas fir type is roughly paralleled by the 4-mm. line. Although the area of less than 10 mm. includes a greater portion of this type than that within the 4-mm. line, the former extends southward, strictly along the coast, into chaparral. A superior correlation is found, however, if the 10-mm. line is compared with the eastern boundary of the northwestern hygrophytic evergreen forest of Shreve (Livingston and Shreve, 1921:Frontispiece). This boundary is strikingly coincident with the 10-mm. line except that the 10-mm. line extends southward (strictly coastal) into more xerophytic vegetation.

The western forest vegetation, as here used, is found in areas having v.p.d. values for July between 10 and 29 mm., with only the pinon and juniper types occurring very extensively in more arid regions than 24 mm. It is thought, in fact, that other western forests hold roughly within v.p.d. limits of 20 mm. or less, which approaches the range of transition from eastern forests to tall grassland, in sections where the v.p.d. values are more adequately known. The mountain isolations, however, are designated 24, 22, etc. These lines are established by the records of a few stations located in relatively low parts of these high mountains.

It is obvious that from the oak-hickory region, reaching into Ohio in the northern United States, successively through tall grassland, short grassland, and sagebrush to creosote bush in California and Arizona, we find the vegetation of the United States zoned from east to west according to a successively increasing vapor pressure deficit. In a general way, therefore, the courses of the v.p.d. lines for July roughly parallel the borders of the major vegetation types as established by Shantz and Zon (1924). If there were more stations providing suitable data, it is likely that the correlations would be better.

#### Correlations between Relative Humidity and Natural Vegetation, and Comparisons with V.P.D. Correlations

Unlike the v.p.d. records, relative humidity data do not indicate the same

modifications of the isoclimatic lines according to topography. It was seen that those stations in the Rockies, or near them, showed sufficiently lower v.p.d. values, compared to the surrounding regions, that the v.p.d. lines were determined there with respect to topography. The relative humidity records seem, rather, to indicate that relative humidity is not nearly so variable with altitude as is v.p.d., a fact in accord with Anderson (1936), who stated that v.p.d. is much more sensitive to temperature changes than is relative humidity.

#### EASTERN VEGETATION

As seen in Figure 2, in the southeastern United States relative humidity offers obvious possibilities as an indicator for differentiating between longleaf-loblolly-slash pine, oak-pine, and chestnut-chestnut oak. East of the 48 per cent line (east of oak-hickory) there are four major vegetation regions corresponding somewhat in each case to the relative humidity areas delimited by the 48, 55, and 58 per cent lines. Chestnut-chestnut oak is principally found in areas from 48 to 55 per cent. Oak-pine is found within limits of from 55 to 58 per cent in the Southeast; longleaf-loblolly-slash pine is found entirely above 58 per cent in the Southeast and the northeastern-lakes forest type is above 55 per cent in the Northeast and in the Appalachian Range.

The northeastern-lakes forest type is not as well correlated with relative humidity as it is with v.p.d. This poor correlation can easily be seen by comparing the 14-mm. line for July, of Figure 1, with the corresponding 55 per cent relative humidity line, of Figure 2, as lines paralleling the southern boundary of northeastern-lakes forests. A considerable amount of the northeastern-lakes forests area of Pennsylvania and New York is south of the 55-per cent line, while the boundary is very close to the 14-mm. line in the v.p.d. map. The v.p.d. map has no extension to Lexington, Kentucky, westward from the Appalachians, as is the case with the relative humidity map. The relative humidity extension is not in accord with the vegetation concerned. Neither does the 55-per cent line as well approximate the borders of the northeastern-lakes forests, throughout the Southern Appalachians, as do v.p.d. lines. However, relative humidity more closely parallels northeastern-lakes forests south of Lake Michigan, since the v.p.d. line bears much farther south than does the boundary of the vegetation type.

The complexity of the eastern vegetation, and the small number of stations, may well account for the lack of apparent superiority of either v.p.d. or relative humidity over the other. The presence of the Great Lakes on the north, the Atlantic Ocean on the east, the Gulf of Mexico on the south, winds from the Great Plains on the west and the Appalachian Mountains extending north and south, each with its respective independent effects, makes for a very complex climate in the eastern United States. The vegetation supported by that climate is therefore difficult or impossible to analyze from the standpoint of a single climatic factor.

#### WESTERN VEGETATION

On the basis of relative humidity the arid isolation in California would represent the next driest area in the United States, the isolation of less than 20

per cent in Nevada being the driest. Also, according to Figure 1, the area has a v.p.d. range as high as that of the general sagebrush region. Figure 3c reveals that the area actually has a higher v.p.d. throughout the year than does sagebrush. In Figure 4c the situation is largely reversed, sagebrush having a higher relative humidity complement throughout most of the year than does this bunch grass in California. In this case only July and August showed higher complements for bunch grass than for sagebrush. Since July and August have been the months of maxima, it seems that, either on the basis of relative humidity or v.p.d., bunch grass is a more xerophytic type than is sagebrush, but far less xerophytic than creosote bush. This is contradictory to conclusions of other authors. Weaver and Clements (1929:Frontispiece) class this area with the grassland climatic climax, a type less xerophytic than either sagebrush or creosote bush. Livingston and Shreve (1921) consider the area semidesert, while the entire Great Basin of sagebrush and creosote bush is classed as desert. The area of lowest relative humidity in Nevada is not in the most xerophytic (creosote bush) but in what is apparently the third most xerophytic type (sagebrush). Relative humidity here places a less xerophytic type as the most xeric of all. In contrast, v.p.d. maintains the areas in their proper sequence to correlate atmospheric aridity with the types as they are generally conceded to be according to xerophytism, with the exception of the aforementioned inconsistency.

On the basis of relative humidity, the northwestern hygrophytic evergreen forest, of the Douglas fir type, has relatively the same atmospheric moisture climate as does chaparral. This again indicates the superiority of v.p.d. as an indicator of the distribution of the major vegetation types.

In general, the desert region of Livingston and Shreve (1921), or sagebrush and creosote bush collectively of Figures 1 and 2, is found in areas of less than 30 per cent relative humidity. However, the lines do not vary in their smaller details nearly so closely as the v.p.d. lines with the boundaries of the desert and semi-desert types.

Short grassland, on the other hand, is better correlated with relative humidity than with v.p.d. isoclines. In the main, plains grassland is delimited by a relative humidity line of 30 per cent on the west and one of 40 per cent on the east. Tall grassland and oak-hickory, taken together, have their eastern boundary roughly paralleled by the 48-per cent relative humidity line, though the correlation is not so close as with v.p.d. lines. The extensions of grassland, in Ohio, Illinois, Nebraska and South Dakota, previously referred to, are not nearly so well correlated with relative humidity as with v.p.d. for July.

It is seen from the discussions and from Figures 1 and 2 that both relative humidity and v.p.d. lines are, in general, somewhat correlated with all the major vegetation types of eastern as well as western vegetation. That a single compound factor, such as v.p.d. (embodying temperature and relative humidity, though not at all expressing the full biotic effect of temperature) should present positive correlations with the several major vegetation types is substantial proof of its importance as an ecological factor.

Finally, in contrasting these factors by anticipating the conclusions from

Figures 3 and 4, it may be seen that v.p.d. far surpasses relative humidity in the correlations with the various vegetative types.

It might be noted that both relative humidity and v.p.d. lines for the wettest month (not illustrated here) divide the United States into trans-continental areas which run contrawise to the major biomes, including the most diversified types in a given unit, and exhibiting the rather axiomatic conclusion that the wettest month is not critical with respect to the atmospheric moisture factor.

### Correlations from Annual Curves of Relative Humidity Complements and Vapor Pressure Deficit Values

The superiority of v.p.d. over relative humidity as a correlating factor is exhibited in Figures 3 and 4. These graphs were prepared from the average relative humidity complement and v.p.d. values of all stations within each vegetation type. Only the values for January, March, May, June, July, August, September and November were used in constructing the curves. Each of the 187 weather stations was used, with the exception of those that were borderline between vegetation types; or those located in a minor vegetation type which was not considered; or else located on small isolations of a type.

The curves show the trend of these climatic factors throughout the year and should be invaluable supplements to the maps of the same factors, since the latter represent values for single months only.

The natural vegetative types are arranged according to their ecological

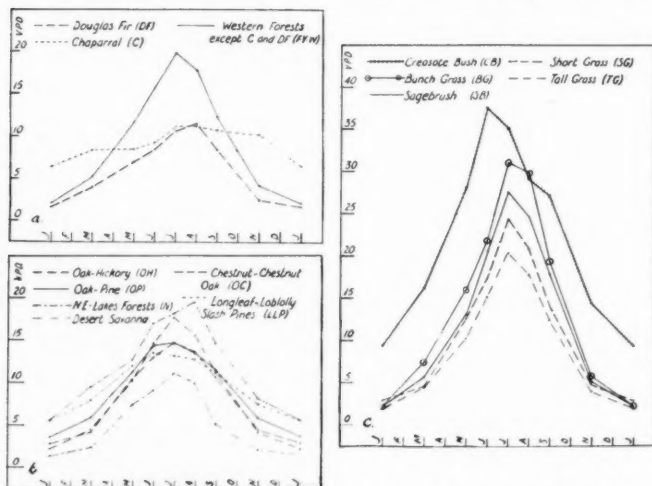


Fig. 3. Annual vapor pressure deficit curves for: a. Western forest types; b. Eastern forest types; c. Interior continental types.



affinity. They are not arranged on the basis of descending v.p.d. for the driest month, although one might easily arrive at such a conclusion.

Figures 3a and 4a each represent all the western forest types; 3b and 4b represent all the eastern forest types; and 3c and 4c represent the very distinctive interior continental types.

The interior continental group comprises all those types of highest atmospheric aridity and of large v.p.d. variation from winter to summer. They are the grasslands, semi-desert, and desert types. The most interesting observation to be made from Figure 3c is that from January to January the curves of only two types cross any of the curves of others. In one case the curve for short grassland crosses that of both bunch grass and sagebrush between January and February and between December and January respectively, revealing that bunch grass and sagebrush have slightly lower v.p.d. values in the extreme winter months and reach considerably higher values during the summer months than does short grassland. In the other case, the curve for bunch grass crosses only incidentally the curve for creosote bush in August, when the value for creosote bush has already dropped markedly from its peak in June. As far as the general trend of the curves is concerned this crossing can be ignored. Throughout the year the vegetation types fall into a series according to a descending v.p.d. value from that of the highest, creosote bush, through bunch grass, sagebrush, and short grassland to tall grassland, the most mesic of all. Bunch grass is not, as Weaver and Clements (1929) claimed, climatically close to short grassland, for it has a v.p.d. higher than that of sagebrush, which is also higher than that of short grassland in this respect. Livingston and

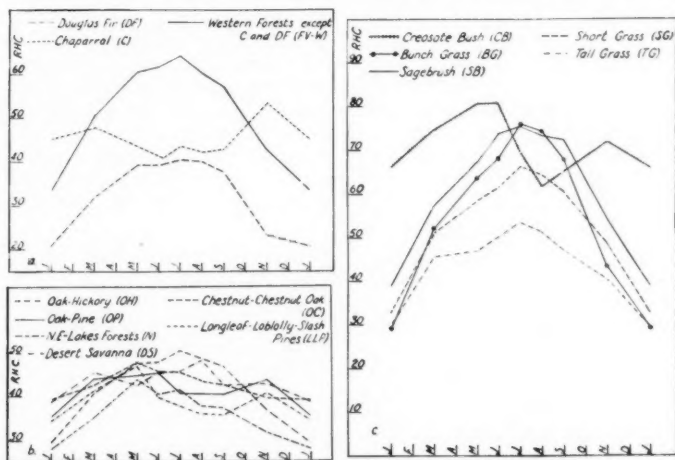


Fig. 4. Annual relative humidity complement curves for: a. Western forest types; b. Eastern forest types; c. Interior continental types.

Shreve (1921) place it in semi-desert, a more probable group, as is indicated by these data. Another noticeable peculiarity is that all interior continental types except creosote bush have virtually the same v.p.d. for the wettest month (January).

These v.p.d. curves may now be compared with the curves for the relative humidity complements of the interior continental grouping. Figure 4 represents the same vegetation group with the types designated by the same lines as in Figure 3. The tendency for a drop in v.p.d. in August for creosote bush is so pronounced in the relative humidity complement curve that, from late June to September, the type has a lower relative humidity complement than either bunch grass or sagebrush. This fact reveals the obvious inadequacy of relative humidity as an index of the xeric nature of a region. It is known that evaporation for this area is higher than in the sagebrush or bunch grass areas, yet the relative humidity is much higher! In spite of a high relative humidity, the v.p.d. values, on the other hand, show that the type is throughout the year subjected to the most arid atmosphere of any type. Here, it is definitely shown that, disregarding temperature, relative humidity means nothing as an evaporation index in nature.

Throughout this paper, heretofore, the data have not been sufficiently unequivocal to warrant a strong disapproval of relative humidity. The reason is primarily that in most cases relative humidities have been accompanied by temperatures that cause the relative v.p.d. values to be not far different from those of relative humidity. From this comparison it can be seen that temperature and relative humidities can simultaneously occur in nature so as to produce v.p.d. values not at all comparable with the existing relative humidities. The variation, from January to January, in relative humidity in the creosote bush area is very slight, when compared with the same variation in v.p.d. All the other types exhibit, seasonally, less marked relative humidity variations than v.p.d. variations. The positions of bunch grass and sagebrush in the two figures are largely reversed, and though no evidence is presented, there is reason to believe in the dependence on v.p.d. and accept bunch grass as the more xeric type. The general trend of the relative humidity curves for the other types corresponds to that of the v.p.d. curves.

Only a glance at Figures 3 and 4 will suffice to see the definite correlational inferiority of relative humidity as compared to v.p.d., with respect to the vegetation of the eastern United States. Desert savanna in Figure 3 is the type of highest v.p.d., whereas in Figure 4, desert savanna varies from next to the highest in August, and highest in March, to lowest in May, with a general irregularity of position throughout the year. The curves for the relative humidity complements can be dismissed without further comparison, for there is relatively no correlation between this factor and the actual xeric or mesophytic nature of the vegetation types concerned as indicated in these curves.

It is seen, however, that the types when arranged according to v.p.d. present a logical sequence. Desert savanna is the most xeric, with oak-hickory less xeric, and oak-pine, chestnut-chestnut oak and longleaf-loblolly-slash pines, respectively, next in line in the summer months. In the winter months they fall

in the order of longleaf-loblolly-slash pines, oak-pine and chestnut-chestnut oak as to highest v.p.d.

The affinity between oak-hickory and chestnut-chestnut oak is seen in the close conformity of the two lines from February to June, and from September to November. The only distinctive difference is during the driest summer months, when oak-hickory exhibits a decidedly higher v.p.d. Longleaf-loblolly-slash pines v.p.d. values reveal the southern and noncontinental nature of this type. The curve shows less extremes from winter to summer, and the values for winter are about as high as for Pacific Douglas fir, but the values for summer are the lowest of all the eastern types except the northeastern-lakes forests.

The v.p.d. curve for the northeastern-lakes forests is logically the lowest of all but even this type is not unique in this respect, when considering the curves for the complement of relative humidity. Also, during the summer months the relative humidity complement curves of desert savanna (the most xeric type of the group), oak-hickory (the next highest for summer) and oak-pine all have lower values at one time or another. There is no logical correlation between the annual relative humidity complement curves for these types.

The curves for the unnatural group of western forests (Figures 3 and 4) are of little significance. One striking peculiarity is that the v.p.d. curve for western forests, except chaparral and Pacific Douglas fir, is identical throughout the year with the v.p.d. curve for tall grassland. Sufficient records would probably reveal different results, but, as previously stated, the range here is a transitional one.

Chaparral is seen to have the most constant v.p.d. throughout the year of any vegetation type in the United States. The curve for the complement of relative humidity shows this type with higher relative humidity in summer than in the spring, fall and winter. If relative humidity is used as the measure of atmospheric aridity, this would indicate that the type is adjusted to winter, rather than to summer drought.

The curve for the Pacific Douglas fir vegetation is similar to that for the northeastern-lakes forests. This is unexpected, for Figure 1 reveals that at least the northwestern hygrophytic evergreen forest<sup>2</sup> of the Pacific Douglas fir type is the most moist of all types, but in these curves it shares this distinction with the northeastern-lakes forests. If data were available for a greater number of stations, this might not be the case.

### Summary

From the discussion of the literature it is concluded that vapor pressure deficit is a more critical ecological factor than relative humidity. Additional evidence is found in the great superiority of the v.p.d. annual curves over the relative humidity annual curves in correlations with the vegetation types. Other evidence is presented in the correlations between the two factors and the distributions of the major vegetation types.

<sup>2</sup> As delimited by Shreve (Livingston and Shreve. 1921).

The general correspondence between the v.p.d. lines for July and the boundaries of the major types of vegetation seems to be too great to be dismissed as a coincidental or secondary correlation.

### Acknowledgments

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## Pollen Spectra from Four Bogs on the Gillen Nature Reserve, along the Michigan-Wisconsin State Line\*

J. E. Potzger

Northern Wisconsin impresses a visitor from central Indiana not only with its decided differences in climate but also by the change in the vegetation, the visible expression of the climate. This is, perhaps, less evident to-day than formerly because the vast forests of conifers which a half century ago covered much of the topography have under pressure of lumbering and fire yielded to scrubby growth of aspen and paper birch, or perhaps even to lowly shrubs of the heath family, and especially to *Comptonia asplenifolium*. There are, however, in Vilas county, Wisconsin, and Gogebic county, Michigan, smaller areas of hardwoods and pine still in their natural, undisturbed condition, where phytosociology is representative of the former greater forest expanses of the region before cultural influences modified them. Here, then, was an unusual opportunity to make a pollen study in bog sediments, and fit pollen records into a vegetation complex of to-day, and thus bring the study of the vegetational tendencies in the region up to the present. Four bogs were included in the study. They are located near the Michigan-Wisconsin state line, on the Gillen Nature Reserve. This reserve is a fine 5,500 acre tract lying partly in Vilas county, Wisconsin, and partly in Gogebic county, Michigan. In its geographical location it is close to the Canadian forest, and character species of the boreal forest are prominent dominants in this southern extension, in relic colonies in bogs and along wet river bottoms. The vegetation as a whole is of the true lake forest type, i.e., pine dominating in sandy, dry areas, and northern hardwoods of yellow birch (*Betula lutea*), hemlock (*Tsuga canadensis*), and sugar maple (*Acer saccharum*) dominating in forests on better loam soils. Beech (*Fagus grandifolia*) has not extended its range so far west. The northern hardwoods was originally very prominent in the area now termed the Gillen Nature Reserve, and pine had a rather scattered distribution. From pollen profiles of Indiana bogs and lakes we were justified to conclude that the broad-leaved phase of the lake forest complex is a more recent invasion than the pine complex, and as stated before, bogs in the Gillen Nature Reserve appeared to be excellently located to fit pollen spectra into representatives of forest primeval still surrounding some of the bogs studied. Here also was an opportunity to check the reliability of pollen spectra in recording forest complexes and forest changes, and to discover when the hardwoods complex first replaced in part the pine dominance. In compliance with the wishes of Mr. Martin J. Gillen, former owner of the reserve, the three deeper bogs were named in recognition of

\* This is contribution 124 from the botanical laboratories of Butler University, Indianapolis, Indiana, and notes and reports 107 from the Limnological Laboratory of the Wisconsin Geological and Natural History Survey, University of Wisconsin.

scientists who have in the past conducted research on this reserve, and the smaller bog near Mr. Gillen's home, was named Killarney Point Bog. The three other bogs studied will, thus, for the first time be named as Birge, Gilbert and Potzger bogs.

The study of vegetational succession during post-Pleistocene times on hand of pollen spectra adds a new significance when records of bogs within the transition lake forest are compared with those from the southernmost limits of Wisconsin glaciation. The worker in peat from Indiana bogs is at once impressed with the "youthful" character of the northern Wisconsin bogs. In the bogs of Wisconsin and northern Michigan the organic deposits are much less consolidated, the peat is coarse and little decomposed. Most mats of the northern bogs are in a quaking state, the present-day vegetation has not entirely lost its boreal aspect, for spruce and fir are still prominent along the periphery and on the bog mats. The average depth of deposits is much less in the north than in the Indiana bogs, where the range is between 32 and 60 feet rather than between 20 and 30 feet as in Wisconsin.

#### The Gillen Nature Reserve

This reserve is a tract of land totalling approximately 5,500 acres; it is located partly in Vilas county, Wisconsin, and partly in Gogebic county, Michigan. Forest primeval covers about 900 acres, the balance consists of cut-over and disturbed former forested land, lakes, bogs, and river valleys. It embodies, thus, vast areas representative of the three forest cover types characteristic of the lake forest, viz., northern hardwoods, pine, and bog forest, the latter dominated by boreal species. Mr. Gillen dedicated the reserve to native fauna and flora, as a place where life may develop undisturbed according to the laws of nature. It is a vast open laboratory where scientists may study native plants and animals, offering fine opportunity for long-period observations without danger of having equipment disturbed. Several projects, of which the pollen study is one, are already in progress, conducted by research workers from Butler, Notre Dame, Chicago and Wisconsin universities. It is hoped that workers from other universities will begin studies in this area. Plans are being made to provide laboratory facilities where chemical and microscopic examinations can be carried out. Enquiries may be addressed to Mr. Martin J. Gillen, Land O' Lakes, Wisconsin.

#### PHYSIOGRAPHIC AND GEOLOGIC HISTORY

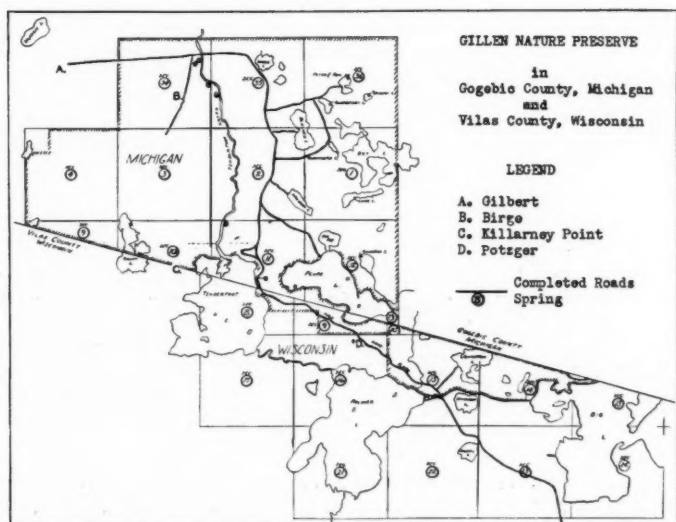
While the region is underlain with strata of the Silurian era, outcrops are few, and so the surface deposits of Pleistocene times alone control and influence the topography and distribution of the vegetation. The topography is of the characteristic irregular glacial type, expressed by moraines and outwash plains. Sandy or clayey ridges and plains alternate with depressions large and small; many of the latter are now filled with water to make lakes or bogs. Some of the smaller, round kettle holes still have a central circumscribed smaller water body, while the long valley-type are completely closed and support forest cover consisting primarily of tamarack and black spruce.

## DESCRIPTION OF THE BOGS

Of the four bogs included, two were of the valley type and two of the small kettle hole type. The latter two (Killarney Point and Potzger bogs) are still in the sedge meadow stage, with *Cladophora* just invading, while the former are forest covered.

## BIRGE BOG

The Birge Bog is approximately three miles in length and a half mile wide. It is located in T. 45 N., R. 42 W., Sec. 33 and 34, Town Marinesco, Gogebic county, Michigan. The peat is well consolidated, but still very wet, and supports a forest constituted of black spruce (*Picea mariana*) and tamarack (*Larix laricina*). The adjacent uplands rise about 20 to 30 feet above the basin. Originally these uplands were very likely covered by a mixed forest of pine and northern hardwoods. At the present the areas are in a stage of secondary succession where paper birch (*Betula papyrifera*) and aspen play a prominent rôle. The surface of the bog is covered by a dense mat of Sphagnum. The peat between surface and 17-foot level is coarse and poorly decomposed. From the 21- to the 29-foot levels sediments consisted of a reddish, finely divided sandy clay with little or no organic matter, and yielded no pollen beyond the 25-foot level. The boring was made as near as possible to the linear center of the basin. Samples were taken at every foot-level to the 29.5 foot depth.





## KILLARNEY POINT BOG

This was the smallest and most shallow of the four bogs, and represented a typical kettle hole. It is located almost on the state line between Tenderfoot and Roach lakes. Its exact location is T. 43 N., R. 8 E., Sec. 7, Town of State Line, Vilas county, Wisconsin. To the north, east and northwest the adjacent areas are rather steep, while the south and southwest borders merge into a wet lowland which in early post glacial times was perhaps an arm of water connecting with Roach lake. This lowland is now covered by a mature stand of hemlock-sugar maple-yellow birch forest (Table 2). The mat of Sphagnum and sedges is still in the quaking stage, while Chamaedaphne and Andromeda are early shrub invaders, advancing in scattered colonies or in lines along old logs. Sediment totalled only nine feet.

TABLE 1.—Stems of trees on one-fourth acre in forest near Potzger Bog.

Species	Size-classes in inches, diameter breast high						Total stems
	1-2	3-5	6-10	11-15	16-20	Above 20	
<i>Acer saccharum</i>	8	8	9	5	1		31
<i>Betula lutea</i>			1	2	3	2	8
<i>Thuja occidentalis</i>			1				1
<i>Tsuga canadensis</i>	7	25	29	3	1	3	68
<i>Tilia americana</i>			2	1	4		7

TABLE 2.—Stems of trees on one-fourth acre in forest near Killarney Point Bog.

Species	Size-classes in inches, diameter breast high						Total stems
	1-2	3-5	6-10	11-15	16-20	Above 20	
<i>Acer saccharum</i>		6	2	6	1	2	17
<i>Betula lutea</i>			5	1	4	7	17
<i>Tsuga canadensis</i>		12	17	7	2	1	39
<i>Tilia americana</i>	1	4	1		2	3	11

## GILBERT BOG

This bog is of the modified valley type, elongated, but set deeply between high ridges. It is located R. 42 W., T. 45 N., Sec. 33. By automobile it is 1.6 miles west of Tenderfoot river on the Nansen lake road. It is about an-eighth mile south of the road in a deep valley. The surrounding sand ridges were perhaps primarily pine or it represented an important part in the original crown cover of the forest, but along the southeastern border northern hardwoods controlled. The mat is well solidified and now supports a medium dense stand of black spruce, tamarack and balsam fir. Sphagnum forms a thick carpet layer.

## POTZGER BOG

The beauty of this deep-set small ice-block type bog immediately attracts attention and interest. The steep slopes rise 40 to 50 feet, ending in flat ridges

which are covered by forest primeval of the northern hardwoods type (Table 1). A small pool occupies the center, while a very quaky mat, barely invaded by trees, covers most of the depression. The poorly decayed and little consolidated peat is coarse and fibrous. The steep flanking slopes indicate that the deepest part of the bowl is beneath the open pool. This suggested the possibility that the boring along the pool's edge may not show the complete profile, beginning with the customary spruce-fir dominance, and present in the completely closed bogs of that region. The bog is located in T. 43 N., R. 8 E., Sec. 16, Vilas county, Wisconsin.

### Methods

Borings were made with the movable sleeve, cylinder-type borer. Samples were as a rule taken at one foot intervals. A small amount of the sediment was removed from the center of the core, placed into a vial and stoppered without addition of a preservative. Each vial was at once labelled with bog designation and foot-level. In the laboratory the peat was dissolved with 95% alcohol, according to the procedure suggested by Miss Geisler (1935), stained with a drop of Gentian violet, and mounted in glycerine jelly. 200 pollen grains were counted of woody genera at each foot-level, except where pollen representation was low. Variations in the count were as follows: Killarney Point: surface, 100; 8-foot, 100; 9-foot, 50. Birge bog: 22-foot, 100; 23-foot, 50; 24-foot, 25; 25-foot, 25. Gilbert bog: surface, 100; 21-foot, 150; 21½-foot, 33. Potzger bog: 30-foot, 100.

### Observations

In a general way, all four bogs show approximately the same vegetational changes, except that in Potzger and Gilbert bogs pine shows evidence of having been a more prominent constituent of the forest while early depositions were in progress (Fig. 1). All bogs show a sudden decline of spruce and a steep rise in representation of pine, a long time dominance, and the entrance of birch and hemlock when the upper half or third of the deposits began to accumulate. In the Killarney Point, Gilbert, and Birge bogs, around whose periphery the original forest has been greatly disturbed or entirely removed, oak shows a prominent increase in the top foot-levels. This marks, perhaps, the initiation of forest denudation by civilized man. Pollen of hemlock reached its maximum representation of 34 percent in the Killarney Point bog. This well reflects the present status of the genus in the forest on adjacent areas (Table 2). The present study for the first time presented an opportunity to the writer to test the validity of representation of such insect-pollinated species as sugar maple and linden. Potzger bog is at present encircled by a magnificent stand of hemlock-sugar maple-yellow birch forest in which linden (*Tilia americana*) has some very old representatives; the same type forest surrounds about three-fourths of Killarney Point bog (Tables 1 and 2). The pollen spectra shown in Figure 1 are, however, striking by the small representation of both maple and linden. This definitely shows that sugar maple and linden do not contribute sufficient pollen to lake and bog sediments to give them the same status of importance

in the pollen spectrum which they held in the forest cover. All four profiles accurately record decline of pine in the region, and the invasion by hemlock and birch. We can perhaps assume that maple was a co-dominant in this broad-leaved forest even though its pollen representation does not justify such a conclusion. We may also be justified to conclude that these pollen spectra accurately indicate climatic moderation which favored the invasion of this region by the broadleaved genera, and initiated the microclimatically controlled "dual" climax of the lake forest. The successive forest complexes have been made up of few genera, where a forest with simple sociological relationships was superseded by a forest constituted of different genera but likewise of simple sociological makeup, which has persisted up there to this day. Broadleaved genera competed successfully with pine since the upper half to one-third of sediments accumulated. It is, of course, a difficult matter to affix time values to such deposits. The lower foot-levels without doubt represent a longer time period than do foot-levels in the upper layers, where the peat is not compressed by the weight of the overlying sediments. Then, too, bogs do not fill in at the same rate in the various locations. Killarney Point bog has only 9 feet of sediments and shows the complete spectrum, including the spruce-fir period, while Birge bog tells a similar story on succession in a 25-foot profile. If the frequently estimated time of 25,000 years for post-Pleistocene is correct, we might say that the invasion by the northern hardwoods in the Gillen Nature Reserve began between 10,000 and 6,000 years ago, perhaps even later. The spruce period apparently dominated for only a few thousand years. The shorter time implied by the one foot of sediment where spruce shows dominance in the Potzger bog as compared with all others in this series merely indicates that the borings at the edge of the open water in the bog did not strike the place of deepest deposition, and thus was omitted a part of the spruce period.

### Discussion

It is rather interesting to note that the early vegetation after retreat of the ice was apparently the same in northern Wisconsin as it had been in late Wisconsin territory in Indiana. The exception is that pine was more prominent and persistent in the Wisconsin region than in Indiana. The Wisconsin and upper Michigan bogs are, however, similar in this respect to those of southern Minnesota, as reported by Artist (1939). In Indiana several foot-levels show only spruce and fir, while in Wisconsin pine is usually associated with these genera. Of course, pine persists longer in Wisconsin than it did in Indiana, where it shows control of the crown cover for only a few foot-levels, as shown by Smith (1937), Moss (1940), Potzger-Wilson (1941), and Potzger-Friesner (1939). The hemlock-birch-maple northern hardwoods apparently never was very prominent in Indiana, but oak became a controlling genus soon after the pine climax had passed, and persisted according to records from most bogs to the present time. While hemlock pollen is usually present in low percentages in all Indiana bogs and lakes, it is never abundant. This was always interpreted by us, Smith (1937), Prettyman (1937) as being due to poor preservation of this pollen, and we referred to Sears (1930) for such conception. We acknowl-

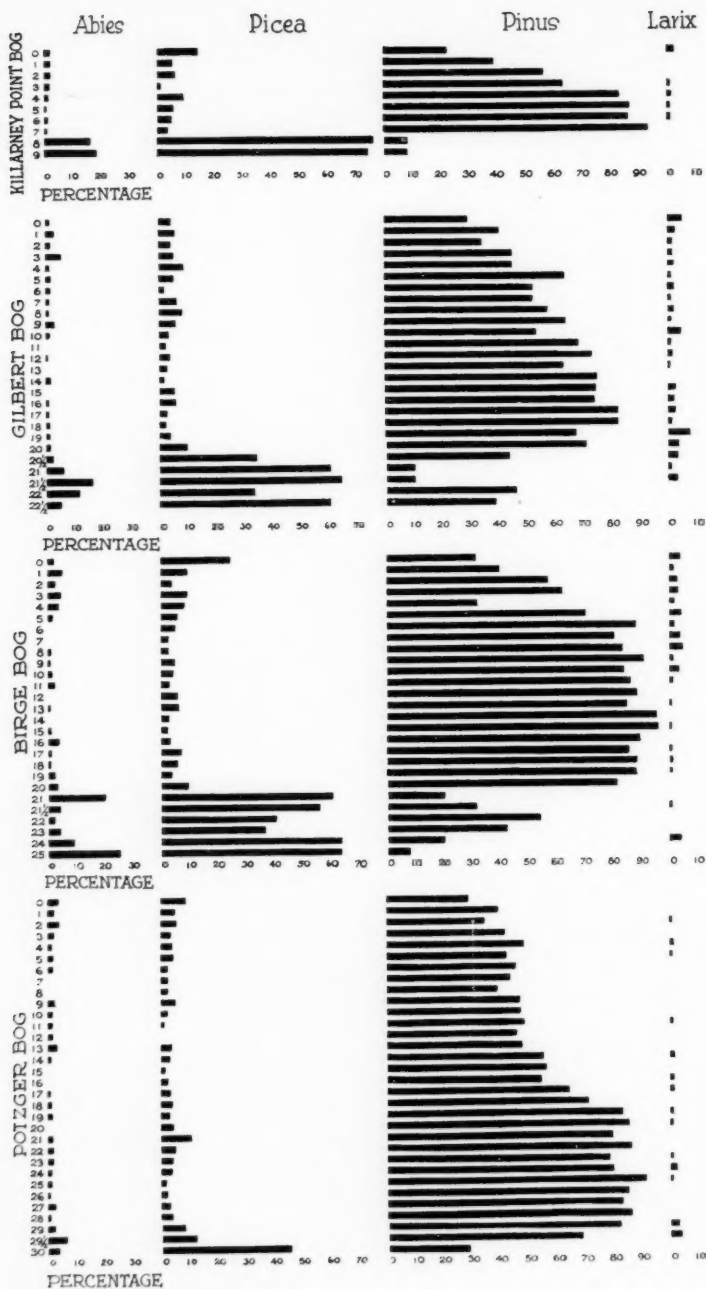
edge our error of having confused *Thuja* with *Tsuga* in the above-named author's publication. The excellent preservation and abundance of hemlock pollen in the Wisconsin bogs, and in the sediments of Connecticut lakes, as reported by Deevey (1939), shows definitely that hemlock pollen preserves well in lake and bog deposits.

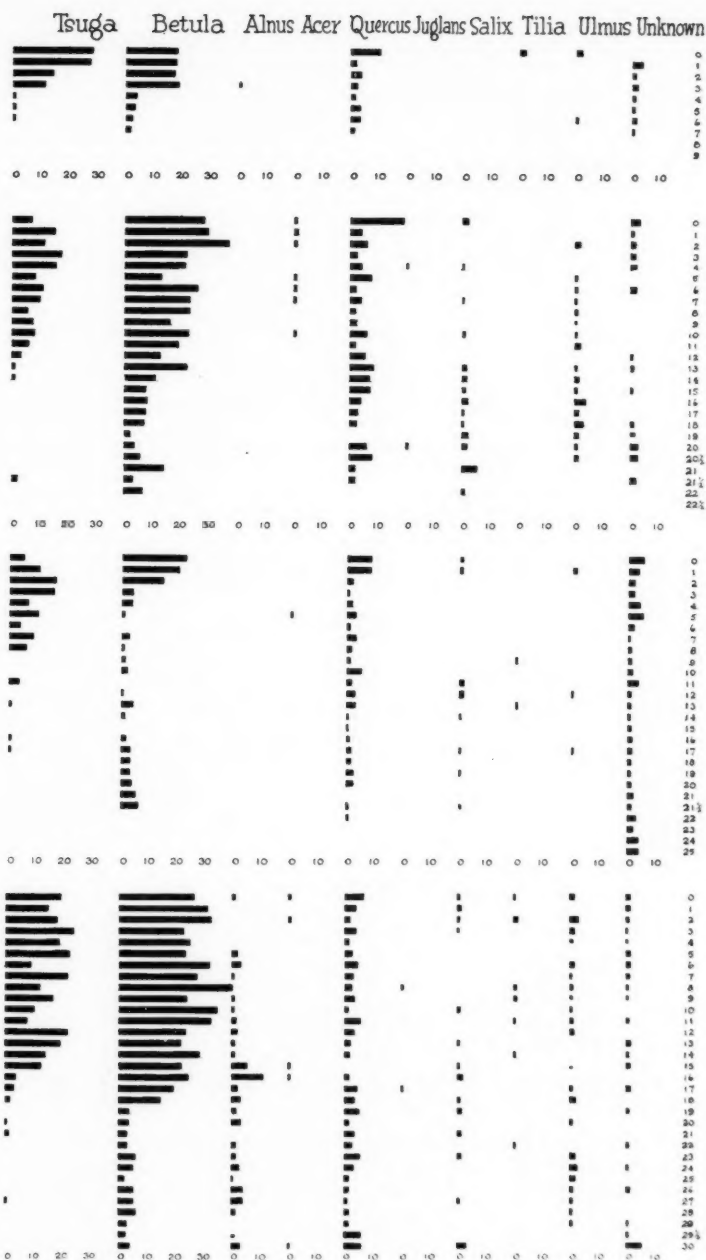
Early residents and lumbermen of the region represented by upper Vilas county, Wisconsin, and lower Gogebic county, Michigan, say that pine had a very scattered representation in the forest primeval of the region, being primarily of the northern hardwoods type. This is also reflected in the upper third of the pollen profiles shown in figure 1. It is very likely that invasion by the broadleaved genera did not occur uniformly in all areas where they now dominate, which is only to be expected, for succession is a gradual replacement in a mature forest and could take place en masse only after a catastrophic destruction of existing vegetation by fire, sleet, or insect pests. If succession takes place without mass destruction of a previous vegetation it would involve a long time, following replacement of individual trees, which would yield to a gradual increase in dominance by the invader and not occur as a sudden replacement. Killarney Point and Birge bogs indicate a more sudden replacement than the Gilbert and Potzger bogs. While oak never reaches a significant representation in this part of Wisconsin, it appeared very early in the vegetation complex (Fig. 1), even earlier than hemlock.

The pollen profiles in the first place give definite information that from a uniform pine dominance, following a spruce dominance, climatic change enabled broadleaved genera associated with hemlock to replace pine in the more favorable soil locations, and so initiate the usually marked "dual" association complex in the lake forest. The climate is favorable to the northern hardwoods but microclimate, controlled principally by edaphic factors, makes possible the persistence of pine dominance, as a second study of bogs about Trout Lake, only twenty-five miles south of the Gillen Nature Reserve, shows, for there pine dominance persisted from the decline of the spruce control to the present day. In the second place these pollen profiles show approximately when this invasion and ecesis took place (Fig. 1).

We cannot well discuss the replacement of pine by hemlock and birch as shown in figure 1 without saying something about the present day association in this hardwood. The forest surrounding Killarney Point and Potzger bogs has sugar maple as very important co-dominant with hemlock and yellow birch, while linden is of secondary importance. As figure 1 shows, maple and linden are sparsely represented in the pollen spectrum, they should, however, be present at least in the top-level since some of the stems in the adjacent forest must be several hundred years of age. This introduces very forcefully the problem of the representation of insect-pollinated trees in peat deposits. A study is planned in the Gillen Nature Reserve which will consider this problem specifically; very likely the pollen of maple and linden is not carried very far from the parent trees.

An old question which usually enters into the interpretation of climatic and vegetational changes is the time element. It is no doubt the most difficult





aspect of the work, as expressed previously by the author (1940). The same difficulty was experienced by Bramlette, M. N and W. H. Bradley (1940) when they attempted to use glacial marine deposits from the North Atlantic as time scales. Bog deposits are perhaps even a little more difficult to use for so definite a mathematical measurement because the weight of the accumulating sediments will warp the uniformity of time in terms of depth of peat, and the ratio in this relationship is not known, and very likely will never be known. In all four bogs of this study the peat was very soft in the upper foot-levels, at times barely sufficiently solidified to provide the resistance necessary to open the sleeve on the borer. Such condition weights the sediment with less years, makes the pollen record of more recent origin than purely proportionally mathematical computations of the total depth of the bogs indicate, so that the upper third may represent at most five to six thousand years; but even this would stamp the northern hardwoods invasion of the region with considerable age.

Pollen profiles point the way to forest planting in sympathy with the climate, and in alignment with natural succession. Since the maple-birch-hemlock forest replaced the pine dominance of many thousands of years standing, it is logical to retain such hardwoods forests in these sites. However, effect of microclimate must also be taken into consideration, in the Trout lake region pine has never been succeeded, as records from four bogs and Grassy lake show in a study by Potzger-Richards (1942). The two studies in Vilas county very definitely show the climatic change which initiated the microclimatically determined pine, and macroclimatically favored hardwoods forest associations in Vilas county, Wisconsin, and Gogebic county, Michigan, area. It furthermore points out that pine was climatically favored for a long period of time. While the pine dominance did not always find expression in regions affected by late Wisconsin glaciation, it did find expression in Indiana at Winona and Tippecanoe lakes (Patzger-Wilson, 1941), Lake Cicott bog (Smith, 1937), Silver lake bog (Moss, 1940) and became more prominent northward from these stations as indicated by the profile from Third Sister lake in lower Michigan (Patzger-Wilson, 1941).

### Summary and Conclusion

1. The paper presents pollen profiles from four bogs on the Gillen Nature Reserve, located in southern Gogebic county, Michigan, and northern Vilas county, Wisconsin.
2. All four bogs show approximately the same forest succession, viz., spruce or spruce-pine to pine to hemlock-birch-pine.
3. Replacement of pine by birch and hemlock took place when approximately the upper half to one-third of the total sediments began to accumulate.
4. The forest primeval adjoining Killarney Point and Potzger bogs has sugar maple equal in importance and abundance to hemlock, but is very sparingly represented in the pollen record. Very likely insect-pollinated species like



sugar maple and linden do not receive sufficient pollen representation in bogs and lakes to reflect truly their importance in the former forest association.

5. Climatically the northern hardwoods is apparently favored, and micro-climate retains pine dominance in forests on sandy habitats.

6. The opinion is expressed that these pollen spectra might well be used as indicators in reforestation projects.

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## Studies in the Genus *Helotium*—II.

### *Lachnum pygmaeum* and the Status of the Genus *Helolachnum*

W. Lawrence White\*

The taxonomic literature on the inoperculate Discomycetes has always been, and still is, so unorganized, and the published species descriptions are so incomplete, that for the general student or even one more or less specialized in the group to find himself confronted with the alternatives of giving his material a new name or not recording it at all appears to be the rule. Attributable perhaps in equal measure to both is the status—taxonomic, nomenclatural, and distributional—of the single species under consideration in the present paper. Though this species very probably is common and widely distributed and certainly is possessed of a combination of characters that should place it among the most easily recognizable of species, it nevertheless has been described as new at least fourteen times and through generic transfers has accumulated some forty-five synonyms, while the total number of collections recorded would doubtless equal little more than half the latter number. For the most part these specific epithets have been preserved from oblivion through the efforts of such compilers as Boudier,<sup>1</sup> Saccardo, and a few others who have perpetuated them in the literature merely as such, and fortunately in a surprisingly large number of cases—in all save two out of the fourteen—by the preservation of the type specimens which have been available for reexamination either by the writer or by some other modern worker, Nannfeldt in particular.

The present study is largely one of synonymy. The generic disposition of the single species involved is largely by arbitrary choice, and until a better basic systematology of the inoperculates permits a more acceptable disposition of the numerous forms now badly placed, perhaps the taxonomic placement of this one species is not important. Many writers, regardless of the name under which they considered it, have commented upon the similarity of certain of its characters to those of species of *Helotium* on the one hand and to those of *Lachnum* or the *Lachneae* on the other. In general aspect it immediately would be referred to *Helotium*. On turning the beautiful and accurate plates of Boudier and finding it among such species as *H. fructigenum* (Bull.) Karst., *H. consobrinum* Boud., and *H. tuba* (Bolt.) Fr. one would scarcely be led to doubt that in a sound phylogenetic scheme it belonged there. Torrend (Broteria 9:53. 1910), believing that he was working with a new species, and noting independently the same characters which had brought so many puzzled comments from previous workers, erected for his form a new genus, *Helolachnum*, and

\* Contribution from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, No. 207.

1 Text references are to be found in the synonymy list.

described the species as *H. aurantiacum*. Should future phylogenetic arrangement necessitate the segregation of this species, either with or without allied forms, then Torrend's generic name will still be available for consideration; its recognition at present however, as distinct from *Helotium* or *Lachnum*, does not appear to serve any useful purpose. On close examination the apothecia are found to be clothed with the rough clavate hairs of the *Lachneae*, however sparse and inconspicuous they may be under a hand lens, to exhibit a pronounced tendency toward the development of long lance-pointed paraphyses, and to have small narrow asci, and small narrow spores—a combination of characters which, together with certain others, set apart those species usually placed in the genus *Lachnum*. Because of these characters the writer supports Nannfeldt's (*Morph. Syst. Discom.*, p. 260. 1932) relegation of *Helolachnum* to synonymy under *Lachnum*, the species to be known as *L. pygmaeum* (Fr.) Bres.

This raises a question of phylogeny and generic concepts in the inoperculates, or more particularly in the families Hyaloscyphaceae and Helotiaceae of the system of Nannfeldt. The problem that is involved in connection with the formidably large genus *Helotium* might be illustrated by an example from the lower Hymenomycetes where evolutionary and taxonomic criteria appear to be less obscure or else where because of greater interest and effort they have come to be better understood. Rogers (*Univ. Iowa Stud. Nat. Hist.* 17:3. 1935), working with the Basidiomycetes, notes that "the genus *Corticium* has perhaps more than any other genus of the hymenomycetes been made up of a heterogeneous accumulation of species having little in common but the lack of any character sufficiently obvious and striking to furnish the basis for segregation." It appears that after obvious characters had been found for the segregation of such genera as *Stereum*, *Peniophora*, *Odontia*, *Radulum*, *Grandinia*, *Sistotrema*, and others—some of them natural and others merely form genera—there was left over a heterogeneous mass of elements of relatively simple morphology which were formerly thrown together in *Corticium*. More recently additional fundamental characters have been found which separate *Corticium* into several series with lines leading into such genera as those mentioned above. It is highly probable that within a certain large group of the inoperculate Discomycetes, *Helotium* occupies a position comparable to that occupied by *Corticium* in the lower Hymenomycetes. That is, it comprises a large assemblage of species, almost surely a heterogeneous lot, held together by a lack of characters: lack of any conical stage, obvious sexual structures, stromata, hairs or markings on the apothecium, teeth or setae on the margin of the disc, tissue differentiation in the context of the disc, differentiation of the paraphyses, or color, septation or sculpturing of the ascospores. The writer has spent some time in studying the lower Hymenomycetes and an even greater amount of time in the helotiaecous fungi, but has failed to find in the latter group any equally valid basis for speculation on the subject of phylogeny and relationships. Assuming that in the systematology of the Helotiales *Helotium* offers to the student of that group problems comparable to those offered by *Corticium* to the student of the Hymenomycetes, it seems that actually the key to their solution is relatively more obscure. Until a more fundamental basis for segregation can be found,

the genus *Helotium* must be recognized in its present broad sense as embracing all the members of the Helotiales that are of waxy texture, are light-colored, have a simple prosenchymatous disc tissue, and lack any sufficiently striking character to place them elsewhere. It will thus to a large extent at least be comparable to *Corticium* and *Polyporus* as these genera have been recognized in America, and perhaps, though not certainly so, will to the same extent be unnatural. If the Hyaloscyphaceae (Nannfeldt), which are characterized principally by having the apothecia clothed with hairs, be considered derived from the morphologically simpler forms now in *Helotium*, then the single much-named species under consideration in the present paper may be considered intermediate in a phyletic series from *Helotium* to *Lachnum*; and it is possible that the genus *Lachnum* or at least the family in which it is placed, the Hyaloscyphaceae, may be derived in several natural series from various sections of our present *Helotium*.

On the following pages is presented a synonymy of the species with a complete literature record as far as is known to the writer, also a brief taxonomic description with certain summarizing data on occurrence and distribution; the thirteen original epithets are then taken up in chronological order and the evidence for their inclusion in the synonymy is presented along with certain other pertinent information. The writer in preparing the paper has not been unmindful of the possibility that future workers may not agree with him on the question of synonymy; an attempt is made therefore to organize the information in such a way that should it become necessary to remove any name from the list, its accompanying data concerning substrata, distribution, etc., may quite easily be removed with it.

After the elimination of numerous species that obviously belong in other genera there still remain in *Helotium* at least five hundred species that will have to be allowed to stand as valid until they can be reworked and reduced to synonymy or shown to belong elsewhere. The taxonomic criteria that are available for the delimitation and identification of these species are few and are of a type that may not be relied upon too closely; they are chiefly size, shape, and color of the apothecium, and size and shape of the ascospores. When a monograph of the group is finally prepared, such lists of synonymy as the one presented in this paper in all probability will not be uncommon.

LACHNUM PYGMAEUM (Fries) Bresadola, Ann. Myc. 1:121. 1903

*Peziza pygmaea* Fr. Syst. Myc. 2:79. 1822; Fr. Summa Veg. Scand. 351. 1849; Berk. & Br., Ann. Mag. Nat. Hist. 3: 15: 445, pl. 15, fig. 18a-b. 1865; Berk. Trans. Linn. Soc. 25: 432, pl. 55, fig. 7-13. 1866; Cooke, Handb. Brit. Fungi 679. 1871; Quél. Champ. Jura et Vosges 2: pl. 5, fig. 5. 1873; Bucknell, Proc. Bristol Nat. Soc., n.s. 4(1): 58. 1883.

*Helotium luteolum* Currey, Trans. Linn. Soc. 24: 153, pl. 25, fig. 11-12, 18. 1864; Berk. & Br. Ann. Mag. Nat. Hist. 3: 15: 446. 1865; Cooke, Handb. Brit. Fungi 710. 1871; Massee, Brit. Fung. Fl. 4: 240. 1895; Massee & Cr. Fung. Fl. Yorkshire 281. 1905; Buckley, Brit. Myc. Soc. Trans. 6: 346. 1920; Ramsb. Brit. Myc. Soc. Trans. 17: 156. 1932.

*Helotium rhizophilum* Fekl. Fungi Rhen. Exsicc. 1598. 1865; Cooke, Handb. Brit. Fungi 714. 1871; Gill. Champ. Fr. Discom. 156. 1879; Quél. Bull. Soc. Bot. Fr. 26: 234. 1879; Pat. Tab. Anal. Fung. 35, fig. 590a-e. 1886; Quél. Enchr. Fung. 308. 1886; Sacc. Syll. Fung. 8: 251. 1889; Boud. Icon. Myc. 449, fig. a-k. 1905-10; Boud. Hist. Classif. Discom. Eu. 113. 1907; Nannf. Morph. Classif. non-Lich. Inop. Discom. 262. 1932; Povah, Papers Michigan Acad. 20(1934):128. 1935.

*Ciboria rhizophila* (Fekl.) Fekl. Symb. Myc. 312. 1869; Rehm, in Rabh. Krypt.-Fl. 1(3):761. 1893; Migula, in Thomé's Krypt.-Fl. 10(2): 1064. 1913; Nannf. Brit. Myc. Soc. Trans. 23: 240. 1939.

*Helotium pygmaeum* (Fr.) Karst. Symb. Myc. Fenn. I. 214. 1871; Karst. Myc. Fenn. pars prima Discom. 153. 1871; Boud. Hist. Classif. Discom. Eu. 113. 1907; Le Gal, Revue de Mycologie 3: 144. 1938.

*Helotium tuba* (Bolt. ex Fr.) Fr. b. *ochracea* Berk. & Br. nom. nud. Ann. Mag. Nat. Hist. 4: 15: 38. 1875.

*Lachnea pygmaea* (Fr.) Gill. Champ. Fr. Discom. 71. 1897. [Non *L. pygmaea* Sacc. & Syd. In Sacc. Syll. Fung. 14: 755. 1899.]

*Peziza* (*Dasy.*?) *nuda* Phill. & Plowr. Grevillea 8: 101. 1880; Scott. Nat. 6: 124. 1881.

*Helotium* (*Pelastea*) *affinissimum* Peck, Ann. Rep. N. Y. State Mus. 33 (1880): 32. 1883.

*Erinella pygmaea* Quél. Enchr. Fung. 303. 1886.

*Hymenoscypha tuba* (Bolt. ex Fr.) Phill. var. *ochracea* (Berk. & Br.) Phill. Brit. Discom. 126. 1887.

*Hymenoscypha Hedwigii* Phill. Brit. Discom. 130. 1887.

*Hymenoscypha rhizophila* (Fekl.) Phill. Brit. Discom. 144. 1887.

*Lachnella pygmaea* (Fr.) Phill. Brit. Discom. 242. 1887.

*Lachnella nuda* (Phill. & Plowr.) Phill. Brit. Discom. 247. 1887.

*Lachnella luteola* (Currey) Phill. Brit. Discom. 247. 1887.

*Ciboria carniolica* Rehm apud Voss, Zool. Bot. Ges. Wien 37:226, pl. 5, fig. 1a-b. 1887; Rehm, Hedwigia 27:164. 1888; Voss, Myc. Carn. part 3, 211. 1891; Boud. Hist. Classif. Discom. Eu. 106. 1907.

*Helotium rhizogenum* Ellis & Ev. Journ. Myc. 4: 100. 1888; Sacc. Syll. Fung. 8: 250. 1889; Ellis, Cat. New Jersey Pl. 550. 1890; Pound, Clements et al., Bot. Survey Nebraska 4: 42. 1896.

*Helotium Phillipsii* Sacc. Syll. Fung. 8: 220. 1889.

*Phialea Hedwigii* (Phill.) Sacc. Syll. Fung. 8: 260. 1889.

*Phialea affinissima* (Peck) Sacc. Syll. Fung. 8: 272. 1889.

*Dasyascypha pygmaea* (Fr.) Sacc. Syll. Fung. 8: 436. 1889; Massee, Brit. Fung. Fl. 4: 353. 1895; Seaver, Proc. Iowa Acad. 12: 116. 1905; Seaver, Bull. Lab. Nat. Hist. St. Univ. Iowa 6: 97, pl. 24, fig. 3a-d. 1910; Bisby, Fungi of Manitoba & Saskatch. 39. 1938.

*Dasyascypha pygmaea* (Fr.) Sacc. forma *prolifera* (Berk. & Br.) Sacc. Syll. Fung. 8: 436. 1889; Trans. Linn. Soc. 25: 432, pl. 55, fig. 7-13. 1866. As *Peziza pygmaea*.

*Dasyascypha luteola* (Currey) Sacc. Syll. Fung. 8: 440. 1889; Boud. Hist. Classif. Discom. Eu. 119. 1907; Nannf. Brit. Myc. Soc. Trans. 23: 241. 1939.

*Hymenoscypha flexipes* (Cooke & Phill.) Sacc. Syll. Fung. 10: 9. 1892.

*Ciboria pygmaea* (Fr.) Rehm, in Rabh. Krypt.-Fl. 1(3): 760. 1893; Feltg. Vorst. Pilz-Fl. Luxemb. 1(3): 44. 1903; Magnus, Die Pilze von Tirol 387. 1905; Migula, in Thomé's Krypt. Fl. 10(2): 1067. 1913; Dodge, Trans. Wisconsin Acad. Sci. 17(2): 1033. 1914.

*Helotium Hedwigii* (Phill.) Massee, Brit. Fung. Fl. 4: 243. 1895; Boud. Hist. Classif. Discom. Eu. 113. 1907; Nannf. Brit. Myc. Soc. Trans. 23:243. 1939.

*Ciboria ochracea* Masee, Brit. Fung. Fl. 4: 276. 1895; Nannf. Brit. Myc. Soc. Trans. 23: 240. 1939.

*Helotium nudum* (Phill. & Plowr.) Masee, Brit. Fung. Fl. 4:498. 1895.

*Phialea arenicola* Ellis & Ev. Amer. Nat. 31: 426. 1897; Lindsay and Syd. Hedwigia 37(7):36. 1898; Sacc. & Syd. Syll. Fung. 14: 768. 1899.

*Calycina rhizogena* (Ellis & Ev.) Kuntze, Rev. Gen. Pl. 3(2):449. 1898.

*Hymenoscyphus affinisissimus* (Peck) Kuntze, Rev. Gen. Pl. 3(2): 485. 1898.

*Lachnum Hedwigii* (Phill.) Bres. Ann. Myc. 1: 121. 1903.

*Ciboria carbonaria* Feltg. Vorst. Pilz.-Fl. Luxemb. 1(3): 44. 1903; von Höhn. Sitz.-ber. Akad. Wien. 115. Abt. I, 1286 (98). 1906; Vel. Monogr. Discom. Bohem. 1: 219; 2: pl. 22, fig. 12. 1934.

*Lachnum pygmaeum* (Fr.) Bres. Ann. Myc. 1: 121. 1903; Nannf. Morph. Syst. non-Lich. Inop. Discom. 262. 1932; Nannf. Brit. Myc. Soc. Trans. 23: 240, 241, 243, 244. 1939.

*Helotium carbonarium* (Feltg.) Boud. Hist. Classif. Discom. Eu. 113. 1907.

*Helotium pygmaeum* (Fr.) Karst. var. *proliferum* (Berk. & Br.) Boud. Hist. Classif. Discom. Eu. 113. 1907.

*Helotium flexipes* (Cooke & Phill.) Boud. Hist. Classif. Discom. Eu. 114. 1907; Nannf. Brit. Myc. Soc. Trans. 23: 243. 1939.

*Hyphoscypha nuda* (Phill. & Plowr.) Boud. Hist. Classif. Discom. Eu. 122. 1907; Nannf. Brit. Myc. Soc. Trans. 23: 244. 1939.

*Helotium subrubescens* Rehm, Ann. Myc. 7: 524. 1909.

*Helolachnum aurantiacum* Torrend, Broteria 9:53, fig. 1-3. 1910; Sacc. & Trott. Syll. Fung. 22(1): 680. 1913; Nannf. Morph. Classif. non-Lich. Inop. Discom. 260. 1932. Under *Lachnum*.

*Ciboria subrubescens* (Rehm) Dodge, Trans. Wisconsin Acad. Sci. 17(2): 1033. 1914.

*Helotium gramineum* Vel. České Houby 850. 1922.

*Lachnum rhizophilum* (Fekl.) Vel. Monogr. Discom. Bohem. 1: 258; 2: pl. 10, fig. 21. 1934.

Apothecia gregarious or caespitose, typically occurring in a few caespitose clusters of 5-10 surrounded by a few growing singly, stipitate, 2-7 (-20) mm. high, 2-4 (-8) mm. across the disc; disc at first infundibuliform, then spreading and plane; stipe slender, flexuous, usually somewhat thickened just below the disc, pale yellow to flesh-color or dull orange, more or less whitish puberulent, often appearing smooth in the dried condition; receptacle concolorous with stipe and similarly marked; margin rather obtuse, when dried becoming somewhat elevated above the hymenium, finely and obscurely puberulent; hairs of receptacle 20-50  $\mu$  long, clavate, rough, hyaline, 4-6  $\mu$  diam., 1-2 septate; hymenium pale yellow to deep yellow often varying toward orange or apricot, retaining the color on drying or becoming more ochraceous; paraphyses more or less lance-pointed, protruding above the asci, septate, 3-4.5  $\mu$  diam.; asci small, cylindric, 60-75 x 4.5-6  $\mu$ ; spores biseriate, 1-celled, narrow, broadest just above the middle, slightly tapering toward a point at the lower end, round or only slightly pointed above, straight, 7-11 x 1.9-2.4  $\mu$ .

Apothecia arising at ground level on partly buried plant debris of all sorts, especially on roots and rhizomes of grasses and other herbaceous plants and on limbs of both frondose and coniferous trees.

Throughout northern United States, southern Canada, and western Europe including the British Isles.

The species as here recognized, despite its excessive synonymy, is not an extremely variable one. It exhibits some variation in color and in length of stipe apparently due to environmental conditions, but all microscopic characters are constant. It is a matter of common observation that among the stipitate inoperculates the degree of color in the apothecium and also the length of the stipe will vary considerably with light and moisture conditions.

PEZIZA PYGMAEA Fr. 1822

Described under this name by Fries in 1822 and transferred by later writers successively to *Helotium*, *Lachnea*, *Erinella*, *Lachnella*, *Dasyyscypha*, *Ciboria*, and *Lachnum*. The original description was based on a single collection made by Fries and which he records as on the decayed trunk of fir in an open swampy place in the mountains in June, presumably in Sweden. Noteworthy among other early literature records is that of Berkeley (Trans. Linn. Soc. 25: 432. 1866) in which two collections are described and illustrated. One of these, said to be bright apricot when mature, and whitish and tomentose on the base of the stems was noteworthy because of the stipe splitting several times with each subdivision terminated by a disc. It "occurred in swampy places on rotten gorse, frequently coming through the ground, on mosses." In the second collection the surface of one of the cups was described as proliferating to form secondary discs.

During the past seventy-five years perhaps a dozen collections have been recorded in the literature under this specific name, most of them from Europe. A woody substratum has been indicated in all or nearly all cases—either partially exposed roots, or partially buried wood or twigs; in one case fallen pine needles; other hosts named specifically are *Alnus*, *Quercus*, furze, gorse. In North America it has been reported from Wisconsin by Dodge, Iowa by Seaver, and by Bisby from Manitoba. Only Seaver's material has been examined by the writer.

Apparently the Friesian type has been lost. Nannfeldt (Brit. Myc. Soc. Trans. 23:240. 1939) commenting on *Ciboria ochracea* wrote: "This name is a synonym of *Lachnum pygmaeum* (Fr.) Bres. Whether it is the true *Peziza pygmaea* Fr. cannot be decided with certainty, as no specimens from Fries seem to exist." However, since there appears never to have existed any disagreement as to the identity of the species, the writer feels justified in accepting Fries' name as the earliest that has been applied to the species.

Only five collections have been located by the writer under *Peziza pygmaea* or any of its later combinations. Two of these are in the Patouillard Herbarium labeled questionably and are considered by the writer as incorrectly determined; the other three are as follows: Wimbledon, Surrey. May, 1867. C. E. Broome. Rabh. Fungi Europ. 1120 (FH)\*—On exposed roots of *Andropogon*. New-

\* Abbreviations used to designate the herbaria in which the material studied is deposited are indicated in the first paper of this series, *Mycologia* 34: 1942.



field, N. J. July 4, 1886. Ellis. (CUP.—8484)—On buried twigs and roots. Iowa City, Iowa. 1904. F. J. Seaver (CUP-D 483).

The following specimens have been indentified by the writer as *Lachnum pygmaeum*: On rotten wood. Belleville, Ontario. Sept. 10, 1878. Macoun, Can. Fungi 425 as *Peziza longipes* C. & P. (OTB)—On rotten logs. Holderness, New Hampshire. June 30, 1922. D. H. Linder (FH)—On hardwood. Lyon's Falls, New York. Oct. 18, 1936. H. J. Miller, W. L. White et al. (FH)—On rotten oak. Iowa City, Iowa. June 6, 1937. G. W. Martin 5196 (FH)—On bases of dead woody or semi-herbaceous plants. Lake Clear, New York. August 22, 1938. H. H. Whetzel (FH).

#### HELOTIUM LUTEOLUM Curr. 1864

The original description was based on material taken at Kent, England, May 31, 1862, "on a gorse stick, the end of which was sunk in the mud of a pool of water." According to the description and the rather good colored habit sketch provided, the apothecia were caespitose, slender-stipitate, and pale yellow, with the margin "covered with very minute parallel white hairs." The author called special attention to the caespitose habit, branching of the stipe, the "peculiar" paraphyses, and occurrence in a moist situation. Cooke, in his "Handbook" of 1871 reproduced Currey's treatment without comment. Phillips transferred it to *Lachnella* noting that he had examined the type and that "the presence of hairs and acerose paraphyses" convinced him that it did not belong in *Helotium*. Saccardo included it in *Dasyscypha*. Massee in 1895 furnished a more detailed description based on his examination of the type and an additional collection "on branches buried among moss" at Worcester, England, by Carlton Rea in September, 1894. He commented further: "The species is obviously a good *Helotium*, as originally proposed by Currey, in spite of the one deviation presented by the peculiar paraphyses. The minute marginal down is not to be compared with the pilose exterior of species of *Dasyscypha*." Another collection referred to the species was reported in 1905 from Yorkshire by Massee and Crossland. Nannfeldt (1939) examined the type and noted: "This species is—according to the type specimen at Kew and the published illustration—identical with the fungus generally known as *Lachnum pygmaeum* (Fr.) Bres.

The Massee Herbarium in the New York Botanical Garden contains Massee's drawings of Currey's types, the Worcester collection of Rea mentioned above, and drawings and notes of what appears to be insofar as the writer has discovered, a fourth collection referred to the species; it was taken at Worcester in 1896. Examination of the Rea specimen reveals no character that is not typical of *L. pygmaeum*. The apothecia are not at all yellow in the dried condition but are dull orange and more or less griseous; the hymenium is brown. Under a hand lens they appear practically smooth, but under the microscope the short rough clavate hyphal tips are numerous.

Durand at one time studied the species and referred to it several North American collections. He placed it in *Lachnum* but never published the combination.

Following is a summarization of specimens examined under *luteolum*. They are all correctly determined and are referable to *Lachnum pygmaeum*: On decaying wet wood among moss. Wyre Forest, Worcester. Sept., 1894. C. Rea (NY)—On burnt gorse

stems partially buried in moss, etc. Manchester, England. June 8, 1904. A. D. Cotton. (CUP-D 190)—On dead stick. Lick Run, West Virginia. June 16, 1907. C. P. Hartley (CUP-D 6515)—On dead sticks. Lafayette, Indiana. June, 1909. Mrs. A. W. Cole (CUP-D 6812)—On earth-covered roots. Mountain Lake, Virginia. July, 1909. Murrill 458 (CUP-D 9004)—On dead roots mixed with sphagnum in orchid basket. Cornell University Greenhouse, Ithaca, New York. 9 April 1910. Burt Brown. (CUP-D 6998).

#### *HELOTIUM RHIZOPHILUM* Fckl. 1865

Described under this name by Fuckel in 1865 and successively transferred to *Ciboria*, *Hymenoscypha*, and *Lachnum*. The original description was based on German material, the apothecia occurring on the decaying rhizomes of *Koeleria glauca*; and in Europe the name seems to have been used only or largely for the form occurring on grasses. The European distribution includes England (rhizomes of grasses, May); France (*Festuca ovina*, autumn); Germany (*Koeleria glauca*, autumn); Poland (as syn. of *Lachnum pygmaeum*, on roots of herbaceous plants, October); Czechoslovakia (*Koeleria* sp., *Festuca* sp., and *Agropyron* sp.). In North America it has been reported but once "on rotten wood in swamp," Michigan [Povah (1935) as *Helotium*]. The apothecia are described in the fresh condition as gregarious to caespitose with the exterior pale and furfaceous and the hymenium 'vitelline yellow' or clear deep yellow." The various descriptions and illustrations in the literature together with the specimens examined indicate no differences at all between this and the preceding *Helotium luteolum*. Boudier (pl. 489) furnishes a beautiful illustration. Bresadola (Ann. Myc. 1:121. 1903) appears to have been the first to refer this name to synonymy with *Lachnum pygmaeum*; and Nannfeldt and Rehm apparently accept this disposition. The doubt expressed by the various writers as to whether *Helotium luteolum* should be referred to *Helotium* or to the *Lachneae* is equally evident in the writings of those who have dealt with *Helotium rhizophilum*.

Material examined: Fckl. Fungi Rhenani 1598 (FH)—Herb. Barb.-Boiss. 1218 (FH).

#### *HELOTIUM TUBA* (Bolt. ex Fr.) b. OCHRACEA Berk. & Br. nom. nud. (1875)

This name was recorded without description for a form collected "on a heap of decaying vegetables" at Menmuir, England, March, 1874, by M. Anderson. Massee in 1895 raised the varietal name to specific rank under *Ciboria* and furnished a complete description based on his examination of the type. The apothecia according to the description were scattered, slender-stipitate, ochraceous in all parts, with both stipe and receptacle glabrous. This description presumably was based on dried material. The paraphyses were said to be slightly thickened at the apex but there was no mention of their being elongated above the asci and pointed. Though there is little in the description to indicate identity of the form with *Lachnum pygmaeum*, Nannfeldt (Brit. Myc. Soc. Trans. 23:240. 1939) has recently examined the type and has referred the species to

synonymy there without comment on its characters. Known only from the type, no later collections having been referred there.

PEZIZA (DASYSCYPHA) NUDA Phill. & Plowr. 1881

The original description was based on material taken in Scotland and said to be "on the ground amongst moss in a fir woods." It appears that no later collections have been referred here and that the type has been lost. The apothecia were described as scattered, pale orange-red, smooth, 5 mm. high and 2.5 mm. across the disc, with the stipe long and flexuous. It was noted as an "anomalous species, having the long pointed paraphyses not hitherto observed in any section besides *Dasyschyphae*, yet destitute of hairs of any kind that would justify placing it in that section." Later compilers included the form in various genera, depending upon their interpretation of the original description and their own generic concepts. Phillips transferred it to *Lachnella*, Masee to *Helotium*, and Boudier to *Hyphoscypha*. Saccardo for no apparent reason changed the name to *Helotium Phillipsii*. Nannfeldt in his paper on British types says: "No specimen seems to exist of this species, but a water-colour drawing in Phillips' Herbarium (Brit. Mus.) as well as the description indicate clearly *Lachnum pygmaeum* (Fr.) Bres."

HELOTIUM AFFINISSIMUM Peck 1883

Original description based on specimen taken at Albany, New York, in the month of June and said to be growing on "decaying sticks buried in the ground." The apothecia were described as subcaespitose, yellow, with external surface and margin slightly pruinose, and the stipe yellowish and 2.4 lines long. Peck noted more or less correctly that the species resembles *Helotium lutescens* from which it differs in its mode of growth, in becoming more discolored in drying, and in having smaller spores. Examination of the type reveals no characters not typical of those previously discussed for *Helotium luteolum* and *H. rhizophilum*. In the dried condition the hairs on the external parts of the apothecium are closely appressed and scarcely noticeable even under a good lens.

Material examined: Albany, New York. June (1880?). Peck. Type. (CUP-D 5952)—On twigs buried in soil. Cascadilla, Ithaca, New York. June 18, 1900. Durand. (CUP-D 894)—On rotted shaded log. Cantwell's Cliff, Hocking Co., Ohio. June 2, 1918. Bruce Fink. Fink, Ascom. Ohio 869 (CUP-D 10964).

HYMENOSCYPHA HEDWIGII Phill. 1887

Based on an English specimen taken in May at Hanwood, near Shrewsbury, and said to be on the twigs of hazel. The gross characters of the apothecia were described as follows: "Cup stipitate, concave or plane, yellow tinged with orange, margin entire, paler beneath; stem rather long, lower half tomentose, white and enlarged; . . ." Masee transferred the form to *Helotium* but only copied Phillip's description, saying that the species was entirely unknown to him. In 1903 Bresadola reported the species from Poland "ad ligna mucida" in June. He transferred the species to *Lachnum* and furnished a brief descrip-

tion based on his material. According to Nannfeldt (Brit. Myc. Soc. Trans. 23:243. 1939) there are in Phillips' herbarium two collections of the species, both on hazel from Hanwood in 1876, one taken in May and the other in June. The original description appears to have been based on the May collection and this is represented only by a water-color drawing. The June collection is represented by a specimen which, quoting from Nannfeldt "... matches the drawing and description so well that I do not hesitate to regard them as the same species, which furthermore proves to be identical with *Lachnum pygmaeum* (Fr.) Bres. Only one herbarium specimen has been located under the specific name *Hedwigii* and it is correctly referable to *L. pygmaeum*.

Material examined: On rotten logs and sticks. Ann Arbor, Michigan. May 26, 1894. Miss D. Bailey (CUP-D 624, 8361).

#### CIBORIA CARNIOLICA Rehm apud Voss 1887

The original description was based on material collected in Jugoslavia, evidently by Voss, who sent it to Rehm. The latter apparently wrote the description which was later published by Voss. The form was said to be "herdenweise auf von der Erde entblösten Wurzeln (*Quercus*?) im Walde bei Tivoli nächst Laibach, Ende June 1884." Rehm's description indicates identity with *Lachnum pygmaeum*, as does also the habit sketch furnished by Voss. However, Voss' drawings of paraphyses, asci, and spores are not at all those of *L. pygmaeum*, nor do they agree with Rehm's description. Voss (Myc. Carn. p. 211) again treated the species in 1891 and this time reported it "auf Coniferenwurzeln und an den Rhizomen von *Brachypodium sylvaticum* sowie *Carex* sp., welche durch Regen von Erde entblöst wurden, herdenweise." He noted that the species scarcely was different from *Lachnum pygmaeum*. It apparently was this collection or combination of collections which was distributed in Rehm's *Ascomycetes* 903 and cited by Voss. The habitat is indicated on the packet as rhizomes of large grasses and other roots. Examination of this specimen shows it to be entirely in agreement in all respects with the writer's conception of *Lachnum pygmaeum*; it perhaps is slightly more yellowish in the dried condition than some specimens and the excipular hairs are slightly less obvious under a hand lens but microscopically are typical. When Rehm (*Hedwigia* 27:164. 1888) published the list of numbers for his *Ascomycetes* fascicle 19 he noted that according to Bresadola (*in litt.*) the species was identical with *Lachnum pygmaeum*, and he later (Rabh. Krypt.-Fl. 13:760. 1893) definitely referred it to synonymy with that species. No additional literature records or herbarium specimens under the name have come to the attention of the writer.

Material examined: Rehm *Ascom.* 903.

#### HELOTIUM RHIZOGENUM Ellis & Ev. 1888

Described from a specimen taken "on exposed dead roots of *Andropogon*" at Newfield, New Jersey, Aug. 1885. The apothecia were described as pale at first, becoming light yellow, 2-4 mm. high, 1-2 mm. diam., the stipes pale and granulose pubescent, and the disc pale yellow. The type has not been seen but several specimens from the Ellis collection at New York have been avail-

able. They agree in all respects except that the apothecia vary somewhat in color and in the conspicuousness of the pubescence as seen under a lens. In one of the collections the apothecia even in their present dried condition retain perfectly the form and color indicated by Boudier (Icon. Myc. pl. 449) for *Helotium rhizophilum* Fckl. Pound and Clements (Bot. Surv. Nebr. 4:42. 1896) report the species from Nebraska on decorticated branches of *Prunus*. This appears to be the only literature record since the original description.

Material examined: On old roots of *Andropogon* in dooryard. Newfield, New Jersey. July, 1888. (NY; CUP-D8490)—On sticks. Agassiz, British Columbia. May 9, 1889. Macoun 87 (NY; CUP-D 8489)—On twigs of *Prunus americana*. Nebraska. July 4, 1896. Pound & Clements (CUP-D 10874)—On grass roots. Newfield, New Jersey. May 29, 1898 (NY).

#### HYMENOSCYPHA FLEXIPES Cooke & Phill. apud Phill. 1891

Described from an English specimen said to be on decorticated wood. The apothecia were recorded as scattered or caespitose, with pale alutaceous and granular exterior, darker hymenium and long slender stipe. Saccardo placed it in *Phialea* and Boudier in *Helotium*. Nannfeldt in his study of British types wrote: "This is another synonym of *Lachnum pygmaeum* (Fr.) Bres. . . . though the description is very deficient. The substratum is coniferous wood." Presumably he examined the type. No other records under the name are known.

#### PHIALEA ARENICOLA Ellis & Ev. 1897

Described from a collection taken in Delaware, June, 1896, and said to be "on sandy ground. . . ." Described as stipitate, with disc dull orange, 2-3 mm. broad, the outside lighter, uneven, subpruinose, and the stipe stout, a-4 mm. long, substrate, gradually enlarged above, and the same color as the disc. No additional specimens have been identified with the species in so far as can be determined, and it appears to have been mentioned in the literature only twice since the original description. Examination of the type indicates agreement in all respects with Boudier's figures of *Helotium rhizophilum*. The apothecia are attached to plant debris buried in sandy soil.

Material examined: "On sandy ground." Blackbird Landing Bridge, Delaware. June 8, 1896. Commons 2487 (FH; NY).

#### CIBORIA CARBONARIA Feltg. 1903

The original description was based on a specimen from Luxemburg with the habitat and locality indicated as follows: "Auf einem Agglomerat von Erde, faulenden Grashalmen und Graswurzeln, auf alter Brandstelle; Grünwald-Dommeldingen. IX. Ol." All the essential characters of *Lachnum pygmaeum* were indicated in the description: The hymenium was described as egg-yellow; the disc 2 mm. diameter; the stipe 5 mm. long; and the external parts of the apothecium pale yellow with whitish pubescence. In 1906 von Höhnelt after having examined Feltgen's type reported that it agreed so well with Fuckel's description of *Ciboria rhizophila* (Fckl.) Fckl. that it would have to

be considered synonymous. A single apothecium from Feltgen's type is in the von Höhnelt Herbarium. It is slender, of an ochraceous orange color and appears smooth under a lens. Velenovský in his "Monographia Discomycetum Bohemiae" included *Ciboria carbonaria* based on a collection from near Mnichovice. His description however does not indicate identity of his material with that of Feltgen and the record should be discounted; perhaps as much can be said for Velenovský's work in its entirety.

Material examined: Type (FH-H).

#### *HELOTIUM SUBRUBESCENS* Rehm 1909

Described by Rehm from material sent him from Wisconsin by B. O. Dodge; later transferred by Dodge to *Ciboria*. The apothecia were said to be gregarious or thickly aggregated on the thickened bark of decaying roots. They were described as 1-4 mm. across the disc with stipes 1-2 cm. long, the exterior parts glabrous, pale rubescent, dilute alutaceous when dry and whitish pruinose. The apothecia of the dried specimens upon examination are found to be of a somewhat orange-ochraceous color on all parts and externally are sparsely and finely granular with white hairs.

Material examined: Rehm, Ascom. 1852. Type. (FH).

#### *HELOLACHNUM AURANTIACUM* Torr. 1910

Based on material taken in Portugal in the month of March and said to be on the roots of *Ulex europaeus* in a moist sandy place. The apothecia were described as gregarious, 4-7 mm. high, 4-10 mm. across the disc, externally puberulent, and of a beautiful orange color. Torrend's description was recorded in volume 22 of Saccardo's Sylloge. Nannfeldt (Morph. & Syst. 260. 1932) refers the monotypic *Helolachnum* to synonymy under *Lachnum* but does not make a new combination in *Lachnum* for the specific name. No other literature references have been seen. The specimen cited below is too fragmentary for study of the macroscopic characters but microscopic examination leaves no doubt as to the identity of Torrend's species; it may or may not be type material.

Material examined: "Ad radices Ulicis europaei." Alfeite (Portugal). IV-1910. C. Torrend. Torr. Fungi Sel. Exsicc. 171. (FH).

#### *HELOTIUM GRAMINEUM* Vel. 1922

Described from Czechoslovakia and with the original description recorded on *Nardus*, *Koeleria*, and *Festuca*. Velenovský later relegated his species to synonymy with *Lachnum rhizophilum* (Fckl.) Vel. and it is on this basis that the present writer is including it.

The author's thanks are due Dr. David H. Linder of the Farlow Herbarium, Harvard University for aid rendered in various ways, Professor H. M. Fitzpatrick of the Department of Plant Pathology, Cornell University and Dr. Fred J. Seaver of The New York Botanical Garden for making available the material and facilities at their respective institutions.

HARVARD UNIVERSITY,  
CAMBRIDGE, MASS.

# Notes and Discussion

## Contents of Owl Pellets

Homer F. Price

The following is a report on the contents of owl pellets personally taken in north-eastern Indiana and northwestern Ohio during the past four years.

Mr. Philip Moulthrop, assistant mammalogist at the Cleveland Museum of Natural History, has determined the contents of these pellets, while the writer has identified the pellets themselves. This was generally done by identifying the bird that flushed from the roost tree or vicinity of nest directly above the pellets.

Only two Ohio records are given as Mr. Moulthrop has or will prepare a paper on the Ohio pellets.

1. Great Horned Owl:—1 pellet collected in vicinity of Hoagland, Madison Township, Allen County, Indiana, May, 1938.  
*Sylvilagus floridanus mearnsii* (Cottontail Rabbit) ..... 1
2. Great Horned Owl:—several pellets in Mill Grove Township, Steuben County, Indiana, April 18, 1939.  
*Cryptotis parva* (Least short-tailed shrew) ..... 3  
*Peromyscus leucopus noveboracensis* (Deer mouse) ..... 6  
*Rattus norvegicus* (House rat) ..... 2  
*Sylvilagus floridanus mearnsii* ..... 1  
Small passerine birds ..... 2  
Starling ..... 1  
\*Quail or Hungarian Partridge (?) ..... 2
3. Northern Barred Owl:—several pellets in vicinity of Pleasant Mills, St. Marys Township, Adams County, Indiana, March 30, 1939.  
*Cryptotis parva* ..... 7  
*Blarina b. brevicauda* (Short-tailed shrew) ..... 3  
*Peromyscus l. noveboracensis* ..... 5  
*Microtus p. pennsylvanicus* (Field mouse) ..... 12  
Small bird (unidentified) ..... 1
4. Great Horned Owl:—several pellets 2 miles southwest of Aboite, Jackson Township, Huntington County, Indiana, April, 1940.  
*Sciurus hudsonicus loquax* (Red Squirrel) ..... 1  
*Sylvilagus floridanus mearnsii* ..... 1
5. Northern Barred Owl:—several pellets in vicinity of Aboite, Aboite Township, Allen County, Indiana, April 3, 1940.  
*Blarina b. brevicauda* ..... 2  
*Sciurus hudsonicus loquax* ..... 1  
*Microtus p. pennsylvanicus* ..... 6

\* Number 4 shot in pellet containing these remains would suggest game bird. The few bones were quail size.



*Rattus norvegicus* ..... 1  
 \**Sylvilagus floridanus mearnsii* ..... 1  
 I might mention that I failed to find the nest during a period of four years, and that my egg collection contains but fourteen sets of this species, taken during the past 27 years.

6. Short-eared Owl:—several pellets west of Edgerton, Jackson Township, Allen County, Indiana, April 1, 1940.

*Peromyscus maniculatus bairdii* (Prairie white-footed mouse) ..... 5  
*Peromyscus leucopus noveboracensis* ..... 1

7. Barn Owl:—a number of pellets in Williams County, about one mile northwest of Evansport along the Tiffin River (Bean Creek), Ohio, May 14, 1939. These owls have nested in a large sycamore tree for at least 28 years. The tree measures seventeen feet and three inches in girth six feet above the ground. It is sixty-four feet up to the cavity which is large enough for a man to enter with ease. A formidable tree to climb.

*Cryptotis parva* ..... 27  
*Blarina b. brevicauda* ..... 4  
*Peromyscus maniculatus bairdii* ..... 4  
*Peromyscus leucopus noveboracensis* ..... 5  
*Microtus p. pennsylvanicus* ..... 74  
*Synaptomys cooperi stoneri* (Cooper's Lemming Mouse) ..... 1  
*Mus musculus* (House mouse) ..... 1  
 \*\**Sylvilagus floridanus mearnsii* ..... 2

8. Barn Owl:—vicinity of Antwerp, Carvayall Township, Paulding County, Ohio, May 26, 1939.

*Cryptotis parva* ..... 17  
*Sorex cinereus cinereus* (Canada shrew) ..... 1  
*Blarina b. brevicauda* ..... 1  
*Peromyscus maniculatus bairdii* ..... 6  
*Peromyscus leucopus noveboracensis* ..... 13  
*Microtus p. pennsylvanicus* ..... 37  
*Mus musculus* ..... 1  
 Mourning Dove ..... 1

Mr. Moulthrop comments as follows, "Of interest are the large numbers of Least Short-tailed Shrews and the single record of the Canada Shrew in one of the Antwerp (Ohio) pellets. The pellets show that the Common Short-tailed Shrew (*Blarina*) is scarce out your way and that the Least Short-tailed Shrew (*Cryptotis*) is common. It is just the reverse in other parts of Ohio."

Williams County is in the northwestern corner of Ohio, while Paulding County borders Allen County, Indiana on the east.

\* "This is the first record we have for an adult rabbit as Barred Owl prey. Is there any chance that these might be Horned Owl pellets?"

The above comment is by Mr. Moulthrop. It is quite possible that there might have been one or two Horned Owl pellets mixed up with the Barred Owl pellets. Ordinarily I can distinguish between pellets of the two species. The pellets were taken at the base of a dead and hollow tree used for roosting by Barred Owls. I flushed Barred Owls from this tree several times in trying to find their nest.

\*\* Both very young.

## The Water Content of the Fresh-Water Jellyfish *Craspedacusta*

D. W. Dunham

The water content of medusae living in brackish water is greater than that of medusae living in sea-water. Hyman, who investigated the water content of *Aurelia*, concluded from her data and from data given by previous investigators, that the water content of medusae in sea-water of typical salinity was 94.0-96.5 per cent.; in brackish water of less than half this salinity, the water content might rise to 98 per cent. Logically then, fresh-water medusae should contain an even greater water content and the data in the table below indicate that such is the case.

For the present study, forty adult female medusae of the genus *Craspedacusta* were collected in an artificial fresh water pool near Columbus, Ohio. The animals used were pulsating actively and as far as could be determined were anatomically perfect. Their water content was determined as follows. The medusae were blotted on filter paper and immediately placed in previously weighed watch glasses and subjected to dry heat at temperatures varying from 60 to 65 degrees C. for eighteen hours. The drying was completed in a desiccator over concentrated sulfuric acid.

The data on one series of ten specimens are given in Table I. Since the remaining specimens, tested in three lots of ten each, gave similar results, their data are omitted.

TABLE I.

No.	Wet weight grams	Dry weight grams	Per cent. water
1	0.2564	0.0020	99.22
2	0.3075	0.0026	99.15
3	0.2725	0.0027	99.01
4	0.2703	0.0021	99.22
5	0.3342	0.0025	99.25
6	0.3320	0.0032	99.03
7	0.3030	0.0023	99.24
8	0.2837	0.0022	99.22
9	0.2247	0.0021	99.07
10	0.2309	0.0016	99.31

It is evident from these data that medusae of *Craspedacusta* contain more than 99 per cent. water.

<sup>1</sup> Science, 87:166-167.

EVANSVILLE, COLLEGE,  
EVANSVILLE, INDIANA.

## Reviews

THE MORPHOLOGY, TAXONOMY, AND BIONOMICS OF THE NEMERTEAN GENUS *CARCINONEMERTES*. By Arthur Grover Humes. Illinois Biol. Monogr. 18(4):1-105, 4

pls., 1 map, 1942. University of Illinois Press. Price \$1.50.

This is a comprehensive monograph on the nemertean ectoparasites of crabs. The morphology and habits of these highly specialized ribbon worms are discussed in detail, with emphasis on their structural and physiological adaptations to their peculiar mode of life. The general features of development are also described. Of particular interest to morphologists is the unique structure of the male reproductive system; this consists of numerous spermaries which, instead of opening separately to the exterior of the body, as is the case with all other nemerteans, are provided with a single efferent duct opening into the rectum. The sperm are consequently discharged through the anus. This almost incredible modification of the reproductive system is found in no other group of animals.

No less than 26 species of crabs, most of which belong to the family Portunidae, and 1 anomuran have been found to serve as hosts. The sexually mature worms are found only on female crabs which are carrying their egg masses. The eggs of the host serve as food for the parasites. Sexually immature worms live between the gill plates of crabs of both sexes but principally of females. It is uncertain how the worms obtain food while on the gills but it is considered improbable that the proboscis can be everted or that the parasite can obtain blood from the gills of the host. Both among the egg-masses and on the gills the worms secrete cylinders or cysts of tough mucus in which they lie coiled. At the time of ovulation the eggs are deposited within these cysts and are fertilized by sperm emitted by an associated male. Development of the direct type proceeds rapidly.

The young pass through a free-swimming larval stage, whereby they are widely distributed in the water where the crabs live. A very small proportion of the larvae find an opportunity of attaching themselves to female crabs of the species on which they are able to live. The others perish.

The most frequent host on the northeast coast of the United States is the lady crab (*Ovalipes ocellatus*) and on the southeast coast and Gulf of Mexico the blue crab (*Callinectes sapidus*). Only three species of these curiously modified ribbon worms were previously known. They have a wide geographical distribution, one of them being found along the eastern coasts of both North and South America and the shores of Europe, another on the west coasts of America, while the third lives on other species of crabs in Japan. The author adds one new species, from Zanzibar, and a new variety from our southeastern coasts.—W. R. COE, Yale University.

THE SEASHORE PARADE. By Muriel Lewin Guberlet, with illustrations by Jan Ogdén. Jacques Cattell Press, Lancaster, Pa., 1942. viii + 197 pp. \$1.75.

In "The Seashore Parade" Mrs. Guberlet has made a worthy contribution to the non-technical literature on seashore life. This book is obviously intended for the enjoyment of non-technical readers and for the instruction of children in that portion of the lore of ocean life with which they can become most readily acquainted, that pertaining to the animal life of the beaches. The author has skilfully introduced the creatures as though they are on parade between the tides. Throughout she has consistently avoided the introduction of scientific names through the use of names familiar to everyone.

The narrative is in attractive literary style. While personification is not wholly avoided, it is used with sufficient discretion to prevent marring the value of the story as natural history. There are surprisingly few slips in either fact or judgment.

The line drawings, though very simple, impart distinctive, life-like appearances to

the animals in their habitats. The bold poster-type of colored plates gives pleasing color effects.

The reviewer read this volume, not critically as a professional zoologist, but as one who many years ago visited for his first time the Puget Sound region, where the scene of the parade is laid. In the pages and between the lines he found reminders of and again enjoyed the wonders of the distinctive fauna of the Pacific Northwest.—HARLEY J. VAN CLEAVE, University of Illinois.

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THE DIARY OF MICHAEL FLOY JR. Bowery Village 1833-1837. Edited by R. A. E. Brooks. Yale University Press, New Haven, Connecticut, 1941. 269 pp. \$5.00.

Michael Floy Jr. was twenty-five years of age when he began, in 1833, the daily journal of thoughts and activities which he continued for four years, almost to the end of his short life. He was the son of a successful nurseryman and florist, living with his father at "Bowery Village" and working almost every day at the nursery at Harlem. Michael Jr. was a pious young man, an ardent Methodist, and took an active interest in the humanitarian movements of his time. In this period he fell in love and was happily married. He read over a hundred books, most of them religious or devotional in nature. He cultivated actively a rare native ability in mathematics. The interest of his *Diary* to scientists lies chiefly in the record of his mathematical studies and the expression of his fresh and original ideas in relation to the mathematics of his time. The reader of horticultural interests will be delighted by the glimpses given in the *Diary* of horticultural fashions and practices in a period of rapid expansion and of the beginnings of many great nurseries. Above these considerations, however, is the virtue of the book as an unusually frank and illuminating self-revelation. The unpretentious narrative of the young Michael Floy gives the reader the privilege of a real meeting with another mind.

The *Diary* has been edited by R. A. E. Brooks, with an introductory note, annotations and a postscript by the late Margaret Floy Washburn, professor of psychology at Vassar College from 1908 to 1937. The book is published by the Yale University Press in celebration of the seventy-fifth anniversary of Vassar College and in honor of Henry Noble MacCracken.—JOHN T. FREDERICK, Northwestern University.

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